Vocal Recruitment in Dwarf Mongooses (*Helogale parvula*)

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DECLARATION

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Abstract

Vocal communication is important in social vertebrates, particularly those for whom dense vegetation obscures visual signals. Vocal signals often convey secondary information to facilitate rapid and appropriate responses. This function is vital in long-distance communication. The long-distance recruitment vocalisations of dwarf mongooses (*Helogale parvula*) provide an ideal opportunity to study informative cues in acoustic communication. This study examined the information conveyed by two recruitment calls given in snake encounter and isolation contexts, and whether dwarf mongooses are able to respond differently on the basis of these cues. Vocalisations were collected opportunistically from four wild groups of dwarf mongooses. The acoustic parameters of recruitment calls were then analysed for distinction between contexts within recruitment calls in general, distinction within isolation calls between groups, sexes and individuals, and the individuality of recruitment calls in comparison to dwarf mongoose contact calls. Playback experiments were conducted to identify whether individuals were able to discriminate between snake and isolation calls, and between isolation calls of individuals from different groups. The results showed that these dwarf mongoose vocalisations convey information beyond their primary recruitment function. Recruitment calls are functionally referential, having context-specific acoustic distinctions and inciting different behavioural responses. This is in contrast to recruitment calls in banded mongooses (*Mungos mungo*) which differ on the basis of urgency, not context. Isolation calls specifically also inform the receiver about the identity, sex and potential group membership of the caller. The contact calls of banded mongooses and meerkats (*Suricata suricatta*), are also individually distinct and those of meerkats also contain group-specificity. However, banded mongooses do not discriminate between individuals and meerkats do not discriminate between groups. A prior finding showed that dwarf mongooses are able to recognise individuals based on their contact calls. The results of the current study support this as dwarf mongoose receivers are able to distinguish between isolated callers. They bias their response to isolated foreign females. Finally, the acoustic individuality of call types depends greatly on their function and the benefits of advertising identity in each context. Snake calls have a lower individual-specificity than contact calls, which in turn are less specific to caller than isolation calls. This study not only adds to the knowledge available on Herpestid communication, but also presents the first example of sex-bias in the response to mongoose vocalisations. It is also the first study in which isolation vocalisations are directly compared to other recruitment calls.

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Opsomming

Akoestiese kommunikasie is belangrik in sosiale vertebrate, veral diegene wat in dig-begroeide omgewings leef waar visuele seine nie goed werk nie. Geluide dra dikwels sekondêre inligting oor om vinnige en toepaslike reaksies te bewerkstellig. Hierdie funksie is noodsaaklik in langafstand kommunikasie. Die langafstand werwingsroepe van dwergmuishonde (*Helogale parvula*) bied ‘n ideale geleentheid om insiggewende leidrade in akoestiese kommunikasie te bestudeer. Hierdie navorsing het die inligting wat deur twee werwingsroepe (in die konteks van ontmoetings met slange of afsondering) oorgedra word, ondersoek, asook of dwergmuishonde op grond van die leidrade verskillend reageer. Roepgeluide is opportunisties van vier groepe wilde dwergmuishonde versamel. Die akoestiese parameters van werwingsroepe is vervolgens ontleed vir verskille tussen kontekste binne werwingsroepe oor die algemeen, verskille binne afsonderingsroepe ten opsigte van groep, geslag en individu, asook die individualiteit van werwingsroepe vergeleke met dwergmuishond kontakroepe. Geluidsopnames is vir dwergmuishonde teruggespeel om vas te stel of individue tussen slang- en afsonderingsroepe, en tussen afsonderingsroepe van individue van verskillende groepe kon onderskei. Die resultate toon dat dwergmuishondgeluide inligting bo en behalwe hul primêre werwingsfunksie oordra. Werwingsroepe is funksioneel verwysend, m.a.w. hulle het konteks-spesifieke akoestiese kenmerke en hulle lok verskillende gedragsreaksies uit. Dit is in teenstelling met werwingsroepe van gebande muishonde (*Mungos mungo*) wat ten opsigte van dringendheid, maar nie konteks nie, verskil. Spesifiek afsonderingsroepe lig die hoorder ook oor die identiteit, geslag en moontlike groepsverband van die roeper in. Gebande muishonde en meerkatte (*Suricata suricatta*) se kontakroepe is ook individueel verskillend en dié van meerkatte is ook groep-spesifiek. Gebande muishonde onderskei egter nie tussen individue nie, en meerkatte nie tussen groepe nie. ‘n Vorige studie het getoon dat dwergmuishonde individue op grond van hulle kontakroepe kan herken. Die resultate van die huidige studie bevestig dit, aangesien dwergmuishond hoorders tussen verskillende afgesonderde roepers kan onderskei. Hulle reageer sterker op geïsoleerde vreemde wyfies. Laastens hang die akoestiese individualiteit van roepe grootliks van hul funksie en die voordele van bekendmaking van identiteit in elke konteks af. Slangwerwingsroepe is minder spesifik aan die individu as kontakroepe, wat op hul beurt minder spesifik aan die roeper is as afsonderingsroepe. Hierdie studie brei nie net die kennis oor kommunikasie van die muishond-familie uit nie, maar beskryf ook die eerste voorbeeld van geslagsvoorkeur in die reaksie op muishondroepe. Dit is ook die eerste studie waarin afsonderingsroepe direk met ander werwingsroepe vergelyk word.

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Chapter 1:

General Introduction

1.1 Acoustics & information

Animals communicate using auditory, tactile, olfactory and visual signals. A signal is broadly defined as a change in the environment caused or created by the sender which conveys information to and thus impacts the receiver (Endler, 1993).

Vocal communication has been widely studied as acoustic signals are conspicuous and easily obtained. Vocal signalling is particularly important in regulating social interactions and coordinating movement in social species, as these signals are able to carry over large distances and are received by multiple individuals. Information commonly transmitted by vocalisations includes one to several cues about the caller (sender) such as identity, sex, size, condition, rank, age and group-membership; urgency or motivation; and external context or activity such as foraging or movement (Scheumann, Zimmermann & Deichsel, 2007; Fichtel & Manser, 2010; Manser et al., 2014). The transmission of such informative cues has been demonstrated in the vocalisations of multiple species of birds and mammals (Townsend & Manser, 2013).

For example, both the howls of Iberian wolves, *Canis lupus signatus* (Palacios, Font & Márquez, 2007) and 'kweer' calls of apostlebirds, *Struthidea cinerea* (Warrington, McDonald & Griffith, 2015) inform receivers about the identity of the caller with individually-specific acoustic distinction. Arnold and Zuberbühler (2006) showed that alarm calls of male putty-nosed monkeys, *Cercopithecus nictitans*, convey information about the predator which allows receivers to adopt the appropriate antipredator reactions. However, not all studies test whether individuals are able to recognise and respond to the acoustic cues identified via acoustic analyses. Although the structure of alarm vocalisations of great gerbils (*Rhombomys opinus*) differs not only in context between predators but also between callers in terms of their identity,

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group, sex and age (Randall, McCowan, Collins, Hooper & Rogovin, 2005), there is no evidence yet of gerbils utilising these cues. The importance of conducting playback experiments alongside sound analysis is reiterated across studies (Townsend, Hollén & Manser, 2010) and most authors agree that tested acoustic variation within signals must be verified by the response of receivers (and vice versa) in order to understand whether the variation is meaningful (Manser et al., 2014). Several case studies, such as the one by Townsend et al. (2010) on meerkats (*Suricata suricatta*), have found acoustic differences but a lack of response to these cues, which brings their significance into question.

1.2 Communication in the family *Herpestidae*

Mongooses are small, highly vocal carnivores in the monophyletic family *Herpestidae* (Agnarsson, Kuntner & May-Collado, 2010; Manser et al., 2014). The vocalisations each species produce are largely dependent on their social structure and habitat (Manser et al., 2014). For example, species in more densely vegetated environments may need to rely more heavily on acoustic communication than visual signals (Townsend et al., 2010) and would therefore have a larger variety of vocalisations. Furthermore, social species such as meerkats may use more interactive vocalisations such as submissive and playing calls (Manser, 1998; Sharpe, 2005) whereas facultatively social mongooses may choose to forgo acoustic signals when alone (Le Roux, Cherry & Manser, 2008).

There is a general, but not strict, trend that obligate social species have far more vocalisations than do facultatively social and solitary species (Manser et al., 2014). However, most mongooses share certain types of vocalisations. These include various alarm calls; contact (or close) calls; fear and pain screams; pup vocalisations such as begging calls; growls or snarls; barks or spits and recruitment calls (Mulligan & Nellis, 1975: *Herpestes auropunctatus*; Baker, 1982: *Herpestes sanguineus*; Baker, 1988: *Atilax paludinosus*; Palomares, 1991: *Herpestes ichneumon*; Le Roux, Cherry & Manser, 2009: *Cynictis*

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penicillata). Where alarm calls often contain much variation to inform the receiver of external context or urgency (Beynon & Rasa, 1989; Manser, 2001; Manser, Seyfarth & Cheney, 2001), contact calls, which are close-range social calls, are simpler and more often inform receivers about aspects of the caller such as identity (Manser, 1998; Fitch, 2012; Sharpe, Hill & Cherry, 2013). Table 1.1 summarises the information discovered within the vocalisations of the three most widely studied social Herpestids: meerkats (*Suricata suricatta*), banded mongooses (*Mungos mungo*) and dwarf mongooses (*Helogale parvula*).

Out of the five species considered in their review chapter, Manser et al. (2014) note that dwarf mongooses have the largest number of discrete calls with at least 30 vocalisations described to date. However, the information available on Herpestid acoustics is still skewed in favour of meerkats, with very few publications on dwarf mongoose vocalisations.

1.3 Study species: Dwarf mongoose

Helogale parvula is an ideal species in which to study vocalisations and their meaning. Dwarf mongooses are social Herpestids that live in large (up to 30 individuals) cooperatively-breeding groups in the savannah-woodlands of south eastern Africa (Caro & Stoner, 2003; Sharpe, Joustra & Cherry, 2010). The dominant pair monopolise breeding, with group members of higher rank gaining more secondary mating opportunities (Keane et al., 1994; Rood, 1986). The females are the philopatric sex, while subordinate adult males disperse to join other groups (Rood 1990, Sharpe, Jooste & Cherry, 2012). Despite these social differences between sexes, dwarf mongooses display no sexual dimorphism (Clutton-Brock et al., 2002; Sharpe et al., 2012). They are uniformly dark brown in colour and are smaller than other mongoose species, reaching 300g or less at full growth (Rood, 1986; Sharpe et al., 2010; Sharpe, Rubow & Cherry, 2016) (Fig. 1.1). They are therefore one of the smallest carnivorous mammals. The majority of their diet consists of arthropods (Rasa, 1983; Rood, 1990), though they have been observed eating small rodents, birds and reptiles.

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Table 1.1: Overview of information transmitted by vocalisations of three social Herpestids

Species	Call type	Cues	Acoustic distinction	Response	Primary Literature
Meerkat (*Suricata suricatta*)	Alarm	Context/Predator	Yes	Yes	Manser, 2001; Manser, Seyfarth & Cheney, 2001
		Urgency	Yes	Yes	Manser, 2001; Manser, Seyfarth & Cheney, 2001
		Individuality	Yes	No	Schibler & Manser, 2007
	Close/contact	Context	Yes	Yes	Townsend, Zöttl & Manser, 2011
		Group-specificity	Yes	No	Townsend, Hollén and Manser, 2010
		Individuality	Yes	Yes	Manser, 1998; Townsend, Allen & Manser, 2011
Banded mongoose (*Mungos mungo*)	Close/contact	Individuality	Yes	No	Fitch, 2012; Jansen, Cant & Manser, 2013
		Context	Yes	not tested	Fitch, 2012
	Pup & escort	Individuality	Yes	Yes	Müller & Manser, 2008
	Recruitment	Urgency	Yes	Yes	Furrer & Manser, 2009a
		Group-specificity	No	-	Furrer & Manser, 2009a
		Sex-specificity	No	-	Furrer & Manser, 2009a
Dwarf mongoose (*Helogale parvula*)	Alarm	Context/predator	Yes	Yes	Beynon & Rasa, 1989
		Urgency	Yes	Yes	Beynon & Rasa, 1989
	Close/contact	Individuality	not tested	Yes	Sharpe, Hill & Cherry, 2013
	Sentinel	Dominance/status	Yes	Yes	Kern, Sumner & Radford, 2016

'Yes' and 'No' indicate presence and absence of either acoustic distinction and/or response to the informative cue. In some cases either the acoustic analysis or playback analysis for response has not yet been performed, indicated as 'not tested'. Where a cue is tested but there is no distinction, there is no need for playback analysis.

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Dwarf mongooses forage for long periods of the day, travelling far and taking refuge in different termite mounds in their territory almost every night (Rood, 1990; Sharpe et al., 2010). They are highly territorial, scent marking boundaries with cheek and anal glands (Rasa, 1973; Sharpe et al., 2012). Each group defends a territory of about 40 ha, which may overlap slightly with the territories of two or more other dwarf mongoose groups. Inter-group encounters may lead to brief fights between same-sexed individuals or rapid separation of opposing groups (Rood, 1986; Sharpe et al., 2012). Like others in the family *Herpestidae*, they are vulnerable to predation by other small mammals, raptors and snakes (Manser et al., 2014).

Figure 1.1: Photograph of a dwarf mongoose depicting general morphological traits, including size and weight. The dye mark on the left hip identifies this individual as an adult male from the group Koppiekats (code KM102) aged 7 months at the time. The photograph was taken during the course of a project undertaken in 2015, the results of which are published in Sharpe et al., 2016.

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1.4 Dwarf mongoose vocalisations

As dwarf mongooses maintain social contact in dense vegetation, they have developed a sophisticated system of vocal signals. This is mirrored in many other social species where the importance of vocalisations trumps that of visual cues due to their efficiency in transmitting through denser vegetation (Rasa, 1984; Manser et al., 2014). Dwarf mongoose vocalisations include various predator alarm calls, contact calls, aggressive growls, submissive calls, begging calls, specific playing calls, screams, excitement twitters (Rasa, 1984; Beynon & Rasa, 1989) and high pitched recruitment calls that carry over a greater distance. There are few studies that examine these vocalisations, either acoustically and/or via playback experiments. Published studies focus mainly on the alarm and contact calls of dwarf mongooses, possibly due to their common occurrence.

Alarm calls are vocalisations that dwarf mongooses produce upon sighting a predator. The call typically results in group members running for cover, but may also simply act to create awareness of the threat. So far analysis has revealed that alarm calls are context-specific, indicating not only the type of predator sighted, but also the level of risk involved (Beynon & Rasa, 1989). The alarm calls indicate the type of predator as terrestrial or aerial with slight variations in acoustic structure. Risk may incorporate the distance of the threat or species of predator as certain predators are more dangerous than others.

The only dwarf mongoose vocalisation which has been examined for informative cues about the caller is the contact call (Fig. 1.3). This close range call is used to maintain contact between group members while foraging (typically within visual range). The calls are individually distinct and individuals are able to recognise and tailor their responses to the identity of the caller (Sharpe et al., 2013). Sentinel calls, which are a form of contact call used when a mongoose is ‘on guard’, convey information about the caller’s rank and dominance status (Kern et al., 2016). Individuals tend to be biased towards the contact and sentinel calls of alpha individuals, or any group members of higher rank than themselves.

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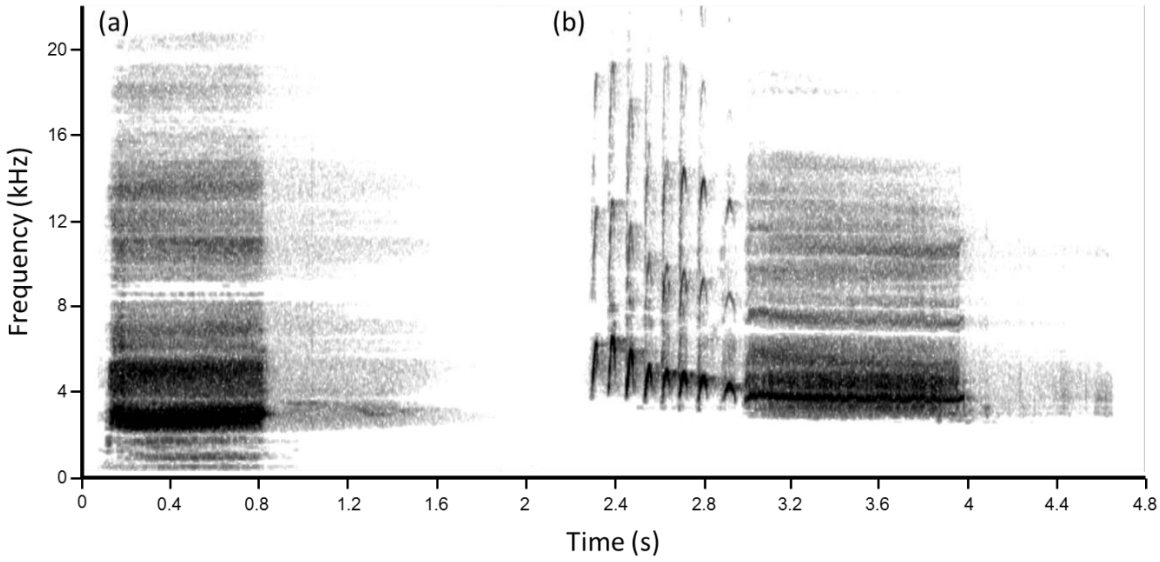

Figure 1.2: Spectrograph of dwarf mongoose (a) terrestrial and (b) aerial alarm calls. Spectrographs were constructed in Raven Lite 1.0 (50% brightness, 60% contrast and spectrogram sharpness 512 pts).

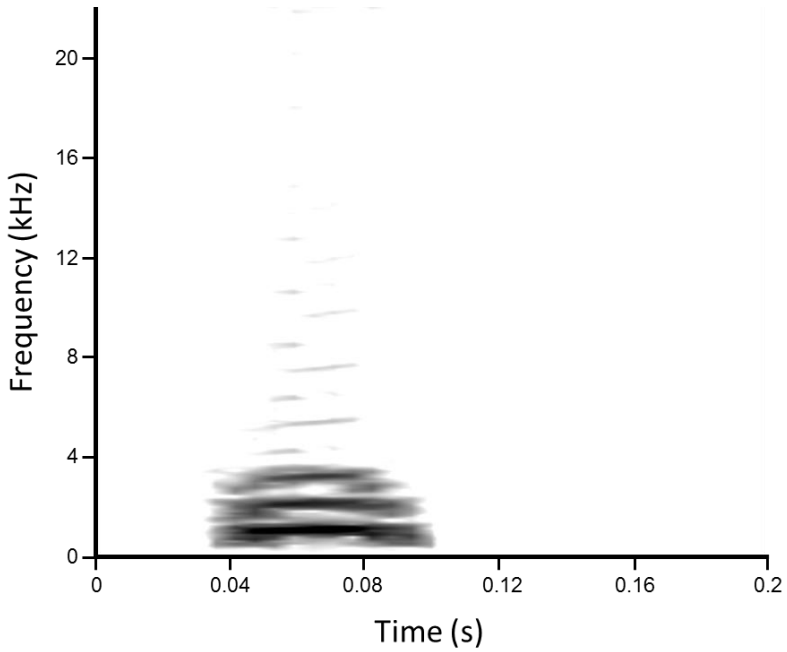

Figure 1.3: Spectrograph of a dwarf mongoose contact call.

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1.5 Dwarf mongoose recruitment calls

Dwarf mongoose recruitment calls are short (48-420 ms), high-pitched (6-10 kHz), monosyllabic, tonal (bandwidth 850 Hz) vocalisations produced at an average amplitude (volume) of 60 dB (for acoustic definitions see Table 1.2). This basic acoustic structure is typical to the recruitment and other conspecific-attracting vocalisations of many species, as explained by Morton (1977). Morton predicts that fearful vocalisations have high-pitched, tonal sounds, in contrast to harsher hostile calls. These vocalisations are also perceived as 'friendlier', as their aim is to attract and obtain aid from conspecifics rather than drive them away - as is the case for more aggressive vocalisations. Furthermore, the high frequency of these vocalisations is ideal for long-distance transmission above the range of lower ambient noises in the environment. This is expected in small animals whose vocalisations are projected at a height close to the ground and surrounding obstructions (Marten & Marler, 1977).

The primary function of recruitment vocalisations in dwarf mongooses is to attract group members to the subject which can be either an external threat (snake) or the caller itself. They are therefore used in several contexts. These include: (a) when encountering a snake to coordinate group movement, (b) when an individual becomes isolated to facilitate its reunion with the group, (c) during inter-group encounters to commence group retreat, (d) to attract potential mates such as roving males or dominant females during oestrus, and (e) to recruit heterospecific co-foragers. While the snake call attracts attention towards a threat as well as the caller, the other types of recruitment call convey purely 'come here' messages. It is unclear whether the calls recruiting the group to the caller (such as isolation vocalisations) and to the location of the threat (to a snake) are context-specific and therefore acoustically different to one another. Nor is it clear whether calls contain secondary information pertaining to the caller's identity. So far there is only one study examining the acoustics of recruitment calls in Herpestids. This showed that the recruitment calls of banded mongooses (to predator faeces, rivals and snakes) inform the audience about the urgency of the situation rather than the context or specific stimulus (Furrer & Manser, 2009a).

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Table 1.2: Basic acoustic terminology

Acoustic Signal	Sound produced in response to stimulus, which has meaning
Ambient noise	All extraneous noise in an environment
Amplitude	The intensity of a sound, measured in the change in atmospheric pressure caused by the sound. Related to volume
Bandwidth	The width of a frequency band (minimum to maximum) at a particular point in time.
Duration	The time, in seconds, from beginning to end of a sound
Formant (F1, F2, F3…Fn)	The harmonic of a note produced by resonance of the vocal tract. There can be several formants at different frequencies above the fundamental frequency
Frequency	The vibration speed, or number of oscillations, of a sound wave, measured in Hertz
Fundamental frequency (F0)	The lowest resonance and perceived frequency of a sound
Inter-call interval	Distance in time between one sound and the next
Noise	Unwanted sound that interferes with a signal
Peak frequency	Frequency at maximum energy of the call
Pitch	The way in which humans perceive frequency. The slower the frequency of a sound, the lower the pitch
Power spectrum	Energy of the call
Range	The maximum minus the minimum frequency across the duration of the sound, in other words the frequency modulation
Wiener Entropy	Measure of the uniformity or tonality of the power spectrum. A pure tone has an entropy of 0 while white noise has a value of 1.

Dwarf mongoose recruitment calls occur rarely (4 natural snake encounters and 30 other recruitment events witnessed in 12 months), making them difficult to sample in a natural environment. The two most common recruitment contexts are when an individual becomes isolated from the group and when an individual encounters a snake. The calls produced in

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these two contexts are indistinguishable to human observers, yet mongooses appear to respond rapidly and differently according to context. This suggests that informative cues beyond simple recruitment are transmitted by these calls.

1.5.1 Snake recruitment call:

Snakes are one type of danger that Herpestids often encounter (Manser et al., 2014). The snake recruitment call, though frequently documented, is not often analysed in acoustic studies. Upon encountering a snake, dwarf mongooses produce both a vocalisation (Fig. 1.4) that sounds like the isolation call (L.L. Sharpe, personal communication, 7 April 2015) to recruit the group and coordinate mobbing, and a distinct spitting call towards the snake itself (Rasa, 1987). This mobbing and spitting call combination has also been noted in meerkats (Graw & Manser, 2007). The snake recruitment calls of both banded mongooses (Furrer & Manser, 2009a) and meerkats (Manser, 2001) have a broad bandwidth with a high percentage of noise and a low fundamental frequency (0-2 kHz). These calls are thus far lower and harsher than those produced by dwarf mongooses, which can partially be explained by the larger body size of meerkats (600-900 g) and banded mongooses (1.5 kg) (Manser et al., 2014). It should be noted that on very rare occasions snake calls have been observed in response to encounters with other threatening animals as well.

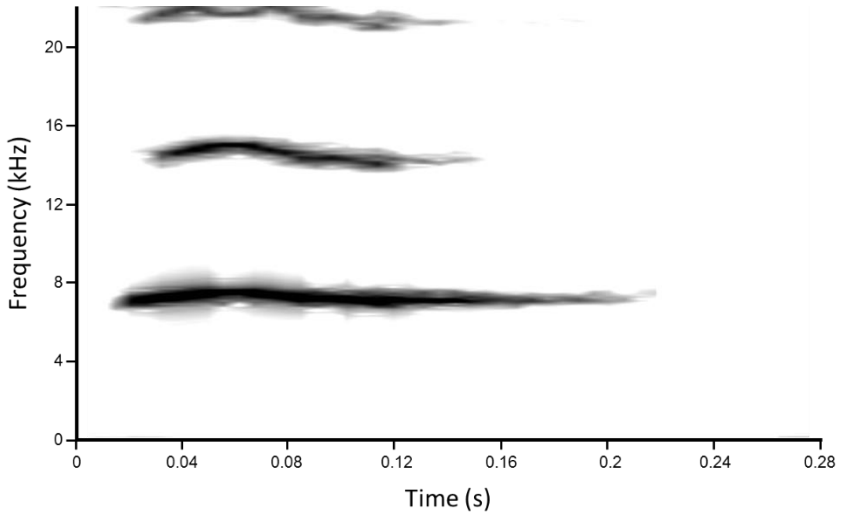

Figure 1.4: Spectrograph of a dwarf mongoose snake call.

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Snake replicas, models and images are often used as a replacement for live specimens when studying recruitment and mobbing behaviour in different species. Though replicas have been successfully used on other species such as common marmosets, *Callithrix jacchus* (Clara, Tommasi & Rogers, 2008), Californian ground squirrels, *Spermophilus beecheyi* (Mitrovich & Cotroneo, 2006) and bonnet macaques, *Macaca radiata* (Ramakrishnan, Coss, Schank, Dharawat & Kim, 2005), when attempted on dwarf mongooses, the mongooses responded with curios investigation and subsequent apathy to the simulated threat. When encountering a live snake however, individuals approach with caution, bob their heads to change perspective and eventually attempt rapid strikes at the snake. Dwarf mongooses may find olfactory cues or a combination of all sensory cues more important than the shape or colour of the object. Odour has been found to be important to other small mammals such as Cape ground squirrels (Phillips & Waterman, 2013) which are able to distinguish between control odours and those of snakes and respond to the latter as if a snake has been encountered. This trend can be seen in meerkats as well. Meerkats mob live snakes for a far longer period than dead snakes, indicating that they are quickly able to assess the level of threat (Graw & Manser, 2007). Therefore, natural encounters with live snakes should preferably be used in studies on snake recruitment calls in dwarf mongooses.

1.5.2 Isolation recruitment call:

When a dwarf mongoose realises that it has become isolated, it begins frantically searching for the group by running around searching for cues and occasionally perching on higher objects for a better view. As time progresses the lost individual will produce more and more isolation calls (Fig. 1.5). Their purpose is to aid the group in locating the lost individual or vice versa. Isolation calls are vocalisations that are well documented because they are both common across mammals and easy to elicit (Scheumann et al., 2007). These calls are usually pure, high in pitch and given at a high rate (Cheney, Seyfarth & Palombit, 1996; Scheumann et al., 2007; Manser et al., 2014). The term ‘isolation call’ (or isolation recruitment call in this study) is often synonymous with ‘distress’, ‘lost’ or ‘separation call’. In dwarf mongooses the

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isolation vocalisation has been noted but never recorded or acoustically analysed. Though there is no mention of an isolation vocalisation in publications on adult meerkats and banded mongooses, the 'weep' (separation call) of the small Indian mongoose (Mulligan & Nellis, 1975) appears to have a similar acoustic structure to dwarf mongoose isolation recruitment calls.

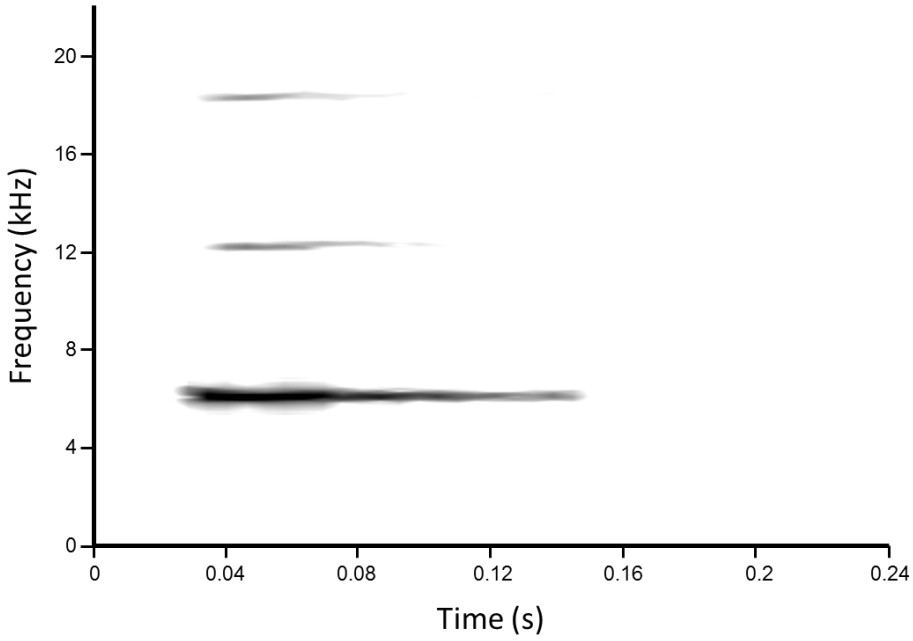

Figure 1.5: Spectrograph of a dwarf mongoose isolation call.

Response to isolation calls may be influenced by the identity of the caller. White-faced capuchins (*Cebus capucinus*) are able to distinguish between the isolation calls of individuals and respond selectively. The isolation calls of dominant males and females are answered more often than those of subordinates, allowing dominants to return to the group faster (Digweed, Fedigan & Rendall, 2007). This study is a rare example examining isolation in adults, as the majority of research focusses on isolated pups and juvenile mammals. It also demonstrates the importance of determining underlying information about the caller within isolation vocalisations.

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1.6 Study population & site

The study population consisted of four habituated groups of wild dwarf mongooses on Phuza Moya Private Game Reserve (E30°45”; S24°15”), Limpopo, South Africa. Data collection for this study took place between March 2015 and March 2016, which constituted a relatively dry year. Study groups, named Bugbears, Ecthelion, Halcyon and Koppiekats consisted of 8, 17, 18 and 21 mongooses respectively. Individuals within each group ranged between 6 months and more than 10 years of age at the onset of the study. Research on these groups began in February 2006, and the mongooses were well habituated to a single researcher observing their behaviour at a distance of 0.5-3.0 meters from the group. Each individual in the study population had a known identity, age, sex, weight and rank and was marked (using a small, long-handled paintbrush) with Garnier Nutrisse blonde hair dye for easy recognition. Neither the chemicals of the hair dye nor the presence of small blonde spots appear to have adverse effects on the mongooses. For the purposes of this study, mongoose behaviour was broadly defined as: ‘Foraging’: nose to ground, scratching and digging with occasional chewing; ‘Social Interaction’: grooming, playing, monitoring pups or sleeping; ‘Vigilant’: head up with an absence of foraging or social interaction or head down accompanied by sniffing or searching behaviour but no scratching or chewing.

The study site in Limpopo is situated in a summer rainfall area with a habitat that is mostly dry woody-savannah consisting of tree species such as marula (*Sclerocarya birrea*), velvet corkwood (*Commiphora mollis*) and knob thorn (*Acacia nigrescens*), above shrubs such as raisin bush (*Grewia spp*.) and bush willow (*Combretum spp*.). The snakes encountered by dwarf mongooses at the study site include the African rock python (*Python sebae*), snouted cobra (*Naja haje*), black mamba (*Dendroaspis polylepis*), Mozambique spitting cobra (*Naja mossambica*) and puff adder (*Bitis arietans*) (Sharpe et al., 2010: electronic supplementary material).

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1.7 Research rationale & Aims

Long-distance calls are particularly important in maintaining contact in social species. It is vital that these vocalisations contain discernible information such as context or identity so that receivers are able to make rapid decisions and aid the caller (Gersick, Cheney, Schneider, Seyfarth & Holekamp, 2015). There is, however, a lack of studies on recruitment vocalisations, and adult isolation calls in particular. This study therefore analyses the vocal recruitment behaviour of a wild (habituated) population in a social species: the dwarf mongoose (*Helogale parvula*), focusing mainly on the information transmitted in isolation and snake recruitment calls.

I aim to demonstrate the informative cues transmitted by recruitment vocalisations and their meaning, by analysing both the acoustic properties (acoustic analysis) of calls and the ability of dwarf mongoose individuals to recognise and respond to these cues (playback analysis). For each informative cue identified I also ask questions regarding the nature and implications of such a cue.

I hypothesise that a) recruitment calls inform receivers about context (snake encounter or isolation) or the urgency of the situation; b) that isolation calls in particular provide information about the identity of the caller; and c) that the level to which snake, isolation and contact calls inform the receiver about individuality varies. These hypotheses will be addressed in chapters 2, 3 and 4 respectively.

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Chapter 2:

Calling for help: dwarf mongoose recruitment calls inform receivers about context and elicit disparate responses

(Accepted by *Animal Behaviour* for publication)

2.1 Abstract

Social complexity and communicative complexity appear to have co-evolved in terrestrial vertebrates. Understanding the information conveyed within the social signals of group-living taxa can illuminate the selection pressures impacting on a species and help to identify the factors promoting sociality. Within vocal communication, recruitment calls are of great importance to many social species, helping to maintain group cohesion and facilitating cooperative behaviour. Yet recruitment vocalisations have received limited scientific attention and it is not clear whether they convey context-specific information to receivers. We investigated the recruitment calls of wild dwarf mongooses (*Helogale parvula*) to ascertain whether they showed context-specific acoustic differences and whether receivers displayed context-specific responses to recruitment calls in the absence of external cues. We recorded recruitment calls (from four wild groups of dwarf mongooses) from two contexts: when an individual became separated from its group, and when an individual encountered a snake. Acoustic analysis revealed that calls from the two contexts differed in acoustic structure and were distinguishable with a discriminant function analysis. Playbacks of calls from both contexts successfully recruited target mongooses, but snake calls elicited a stronger reaction (with mongooses vigilant for longer and approaching the speaker more closely). More importantly, target mongooses also displayed behaviours that were unique to call context, exhibiting head-bobbing, creeping and searching of the vegetation during snake call playbacks

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but never during isolation call playbacks. We conclude that dwarf mongoose recruitment calls refer to context and are perceived as functionally referential by receivers.

2.2 Introduction

In birds and mammals, there appears to be a close tie between social complexity and communicative complexity (Freeberg, Dunbar & Ord, 2012; Pollard & Blumstein, 2012; Manser et al., 2014). As societies become more complex, group members need to communicate more information in order to regulate their interactions and relationships. This promotes the evolution of sophisticated signalling systems which, in turn, allow the development of more complicated social relationships (Pollard & Blumstein, 2012). However, it appears that the development of different aspects of sociality are associated with the development of different aspects of a species' signalling repertoire. For example, in social Sciurid rodents the demographic complexity of the social group predicts alarm call repertoire size while social group size predicts vocal individuality (Pollard & Blumstein, 2012). In Herpestids, social group size seems to influence the number of discrete vocal signals employed, but other aspects of ecology and social complexity also play a role (Manser et al., 2014).

Within the context of vocal communication, one very important social signal is the aggregation or recruitment call. This vocalisation is used by social birds and mammals to reunite separated group members (Miller, Scarl & Hauser, 2004) and/or gather individuals for cooperative defence (Furrer & Manser, 2009a) or group movement (Gruber & Zuberbühler, 2013). Separation or isolation recruitment calls are of considerable importance in fission-fusion societies where group members often disperse widely (e.g. spotted hyaenas, *Crocuta crocuta*: Gersick, Cheney, Schneider, Seyfarth & Holekamp, 2015) or after accidental separation within more cohesive societies (e.g. white-faced capuchins, *Cebus capucinus*:

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Digweed, Fedigan & Rendall, 2007). Calls to recruit group members for cooperative defence may be given in response to predators (Manser, 2001) or competitors, including intragroup (Slocombe & Zuberbühler, 2007), intergroup (Furrer & Manser, 2009a) or interspecific rivals (Gersick et al., 2015). Despite the critical role that recruitment calls play in maintaining group integrity and facilitating cooperation in many social vertebrates, the acoustic structure of these vocalisations has received limited scientific attention.

The recruitment function of recruitment calls has been demonstrated experimentally in a number of studies (Evans & Evans, 1999; Manser, Seyfarth & Cheney, 2001; Radford & Ridley, 2006; Welbergen & Davies, 2008; Furrer & Manser, 2009a; Kennedy, Evans & McDonald, 2009; Suzuki, 2012; Gruber & Zuberbühler, 2013; Kern & Radford, 2016). Nevertheless, the level of responsiveness shown by individual group members often varies (Digweed et al., 2007, Gersick et al., 2015), presumably because individuals differ in the costs and benefits they accrue from responding. For group members to accurately evaluate these potential risks and benefits, they need to obtain information about context. This may be derived directly from external cues (Wheeler & Fischer, 2012) or from acoustic cues within the recruitment call (Furrer & Manser, 2009a).

Much of the research on recruitment vocalisations has focussed on the information that these signals convey about the caller. The recruitment calls of certain species inform receivers of caller identity, status, sex, kinship or degree of arousal (Gouzoules & Gouzoules, 1990; Kennedy et al., 2009; Scheumann et al., 2012), all factors that may impact on a receiver's decision to respond. For example, the long distance recruitment call of cottontop tamarins, *Saguinus oedipus*, informs receivers of caller sex and group members bias their response to the opposite sex (Miller et al., 2004). Both spotted hyaenas (Gersick et al., 2016) and white-faced capuchins (Digweed et al., 2007) can ascertain caller rank from recruitment calls and respond more readily to dominant individuals. Dwarf mongooses (Kern & Radford, 2016) and

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crested macaques (*Macaca nigra*; Micheletta, et al., 2012) respond more strongly to the recruitment calls of group members with whom they share close bonds.

In addition to details about the caller, information about external context is likely to play a critical role when an individual is deciding whether to respond to a recruitment call. This is particularly so in taxa that use one recruitment call in a variety of situations. Spotted hyaenas for example, use recruitment whoops to muster support during both intergroup and interspecific conflicts (Gersick et al., 2015), cottontop tamarins reunite lost group members and attract mates with their combination long call (Miller et al., 2004), and both meerkats (*Suricata suricatta)* and banded mongooses (*Mungos mungo*) use their recruitment call when mobbing snakes, investigating secondary predator cues and repelling conspecific intruders (Manser, Bell & Fletcher, 2001a; Furrer & Manser, 2009a). These contexts vary considerably in the degree of risk they impose, which could significantly impact on an individual's decision to participate in cooperative activities. Under such circumstances, we would expect selection to promote the evolution of recruitment calls that convey contextual information. Few studies, however, have examined whether the acoustic structure of recruitment calls is context-specific. For a signal to be 'context-specific' it should be structurally unique, referring only to a particular situation or stimulus (Scheumann, Zimmermann & Deichsel, 2007). To be 'functionally referential', this information must also be perceivable by others, i.e. specific to both context and response-type (Macedonia & Evans, 1993; Townsend & Manser, 2013).

Attempts to ascertain whether recruitment calls provide specific information about their external stimuli have largely been limited to studies of avian mobbing calls. Mobbing calls differ from alarm calls in that they recruit group members *to* a potential threat instead of causing them to flee a threat. Eight species of group-living bird are known to produce mobbing recruitment calls that convey contextual information (reviewed in Suzuki, 2016), but only in two instances are these calls functionally referential. The mobbing calls of Siberian jays (*Perisoreus infaustus*) differ acoustically with predator behaviour (Griesser, 2009), and those of Australian magpies (*Gymnorhina tibicen*) differ with predator type (Kaplan & Rogers, 2013).

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In both species, receivers respond to these distinct mobbing calls with different behaviours. In the other six avian species, mobbing calls (and the receivers' response) differ in intensity only and reflect the arousal (or anxiety) of the caller (influenced by the type, size and proximity of the predator) rather than referring to the specific context (Suzuki, 2016). Meerkat recruitment calls, elicited by snakes versus predator faeces, also appear to signal urgency (or arousal of the caller) rather than stimulus type, even though this species employs functionally referential alarm calls (Manser, 2001; Manser et al., 2001a).

Only one study has compared recruitment vocalisations elicited by predator and non-predator stimuli. Furrer and Manser (2009b) examined the acoustic structure of banded mongoose recruitment calls elicited by snakes, predator faeces and intergroup encounters. They found that, although calls differed acoustically between these three contexts, the differences were graded and appeared to be urgency or arousal-based rather than context-specific. Similarly, although group members responded more strongly to the playback of calls recorded in high urgency contexts, their behavioural response (cautious investigation) did not differ between contexts, indicating that they were not functionally referential.

In this study we examine whether the recruitment calls used by dwarf mongooses (*Helogale parvula*) convey information about external context. Dwarf mongoose are small (200-300g), social carnivores that live in cooperatively-breeding groups - of up to 30 individuals - in the savannah woodlands of Africa (Sharpe, Joustra & Cherry, 2010). Foraging with their groups in (relatively) dense vegetation, this species has a sophisticated system of vocal signals. These include 'close' contact calls to maintain group cohesion, twitters to indicate excitement (Beynon & Rasa, 1989), functionally referential alarm calls (Beynon & Rasa, 1989) and a high-pitched recruitment call to attract conspecifics (Kern & Radford, 2016).

The recruitment vocalisation is used in five different contexts: to reunite lost group members, to coordinate group retreat during rival encounters, to attract potential mates, to muster group members for the cooperative mobbing of snakes and to recruit heterospecific foraging

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partners. The recruitment calls employed in these five contexts are identical to the human ear, yet receivers respond quickly and appropriately according to the context, suggesting that calls may transmit informative cues of context or urgency. We compared recruitment calls elicited in the two most commonly occurring contexts (snake encounter and isolated individual) to answer three questions. First, are there acoustic differences between recruitment call types (snake versus isolation) which may act as cues of context? Second, do dwarf mongooses respond appropriately to recruitment calls elicited in these two distinct contexts, in the absence of external cues? Third, are the recruitment calls functionally referential with regard to context, as opposed to being graded in response to urgency? We undertook both acoustic analyses and playback experiments to address these questions.

2.3 Methods

2.3.1 Sound recording:

We recorded recruitment calls opportunistically from dwarf mongoose adults in four wild groups on Phuza Moya Private Game Reserve (24°16'10''S, 30°47'46''E) between March 2015 and 2016. This population has been studied since 2006. Groups are habituated to an observer walking or sitting near (>0.5 m) them. Each individual is marked with hair dye for individual identification. All vocalisations were recorded at a distance of 0.5-3 meters from the caller to ensure the quality of recordings and accurate identification of the caller. We recorded vocalisations with a Marantz PMD-670 solid state recorder (Marantz, USA) and Roland R26 portable recorder (Roland Corporation, Japan) with Sennheiser directional microphones (model ME66/K6; Sennheiser electronic GmbH & Co., Germany) and windshields. We obtained Isolation calls by following the mongoose groups during morning foraging hours on sunny, relatively windless (<11 km/h) days and recording the calls of any mongoose that became separated from the group. Snake recruitment calls were also recorded opportunistically when groups encountered a snake. At the study site in Limpopo, South Africa,

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the snakes dwarf mongooses may encounter include: the Mozambique spitting cobra (*Naja mossambica*), African rock python (*Python sebae*), snouted cobra (*Naja haje*), black mamba (*Dendroaspis polylepis*) and puff adder (*Bitis arietans*) (Sharpe et al., 2010). During the study period only encounters with puff adders were witnessed. We recorded vocalisations from the closest possible safe distance and, where possible, took photographs of the snake (Nikon D5200 DSLR camera; Nikon, Japan) for later identification. However, due to the limited number of such encounters; we had to create a snake encounter artificially for three of the four groups. An adult (>4 years) male puff adder was brought from the Hoedspruit Kinyonga Reptile Centre and presented to each of the three groups separately. The puff adder was placed inside a wire mesh container in a shaded area where puff adders might naturally occur, within the trajectory of the foraging mongoose group. This setup enabled olfactory, visual and auditory cues without endangering individuals of either species. We began recording recruitment calls once the snake was in place, noting the identity of the caller where possible. Only calls from known individuals were later used for analysis. We terminated recording once the mongooses had lost interest and moved past the snake. A staff member from the reptile centre was present at all times to monitor the condition of and transport the snake. All experimental procedures were approved by Stellenbosch University's ethics committee (SU-ACUD16-00016) and conform to South African laws.

We digitised all recordings in .wav format (16 bit, 48 kHz) and used Adobe Audition 2.0 to isolate single calls and prepare them for playbacks. We isolated 875 isolation calls (from 38 individuals) and 666 snake calls (from 38 individuals). Only callers > 6 months old were included. To compare snake and isolation calls, monosyllabic calls from the same individual were used, and the sample was limited to those callers with sufficient, high quality examples of both call types available (16 individuals). We considered calls to be high quality when they had no obscuring sounds and two or more clearly visible formants (Fig. 2.1). All snake recruitment calls were elicited by puff adders. We then used this sample of calls both for acoustic analysis and to prepare playback experiments.

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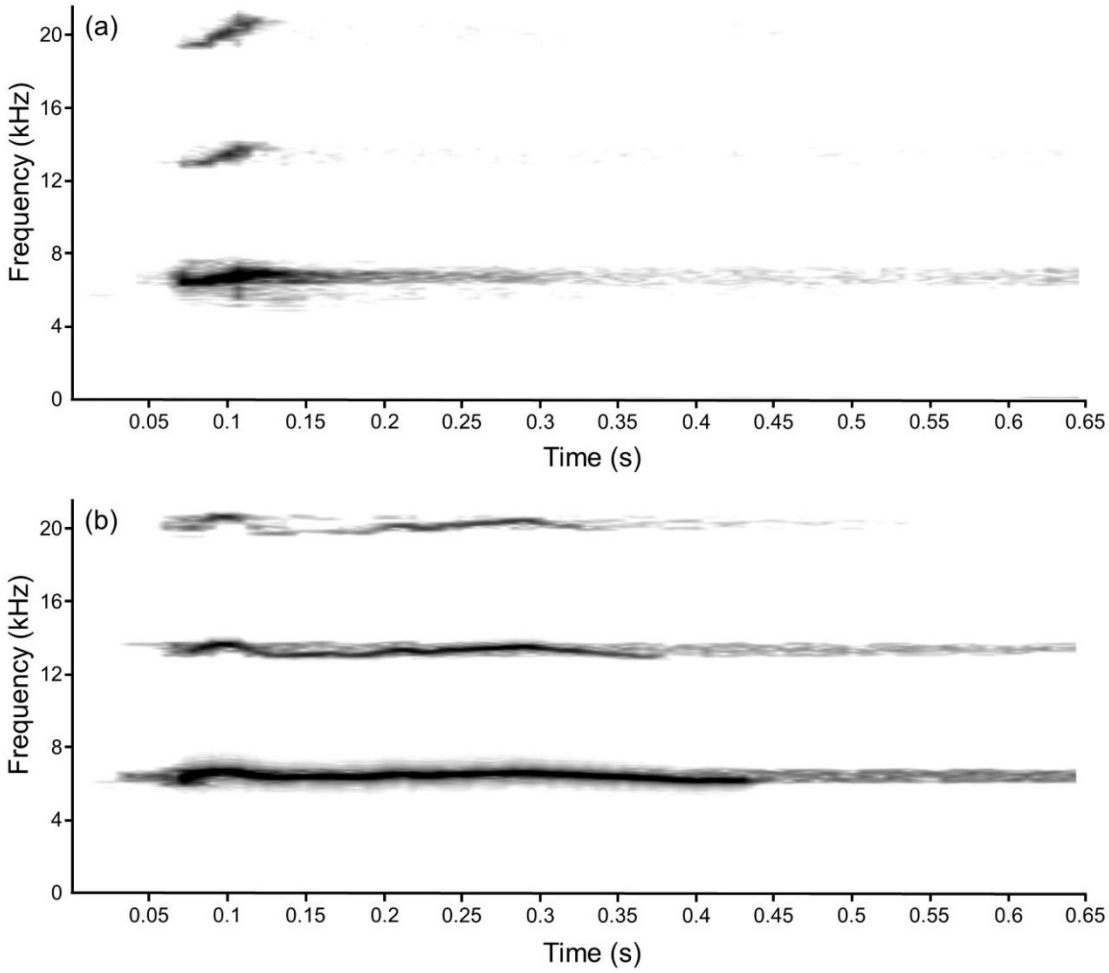

Figure 2.1: Spectrographic comparison of (a) an isolation and (b) snake recruitment call of an adult male dwarf mongoose (HM048). Spectrographs were prepared in Raven Lite 1.0 (50% brightness, 60% contrast and spectrogram sharpness 512 pts)

2.3.2 Sound analysis:

Acoustic parameters from the calls of 16 adult mongooses were computed with Luscinia bioacoustics software (RF Lachlan version 2.0) by Fast Fourier Transformation (1024 points, Hamming Window, time step 0.36 ms, frame length 23.22 ms & overlap 98.45%). We then chose a subset of 28 commonly used parameters for statistical analysis. For the fundamental frequency (F0), we measured the duration; quartiles and variance of the power spectrum (Q1, Q3 and PS variance); and Wiener Entropy (mean, median, start). For both the fundamental

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and the first formant (F1), we measured the mean frequency; maximum frequency (overall, mean and median); the peak frequency (mean, max and start); the time at which the maximum peak frequency occurs; mean bandwidth; and range (maximum-minimum frequency). Additionally, we calculated the gap, or formant dispersion, between the two formants (F1 mean – F0 mean). See Fig. 2.2 for examples of parameters measured.

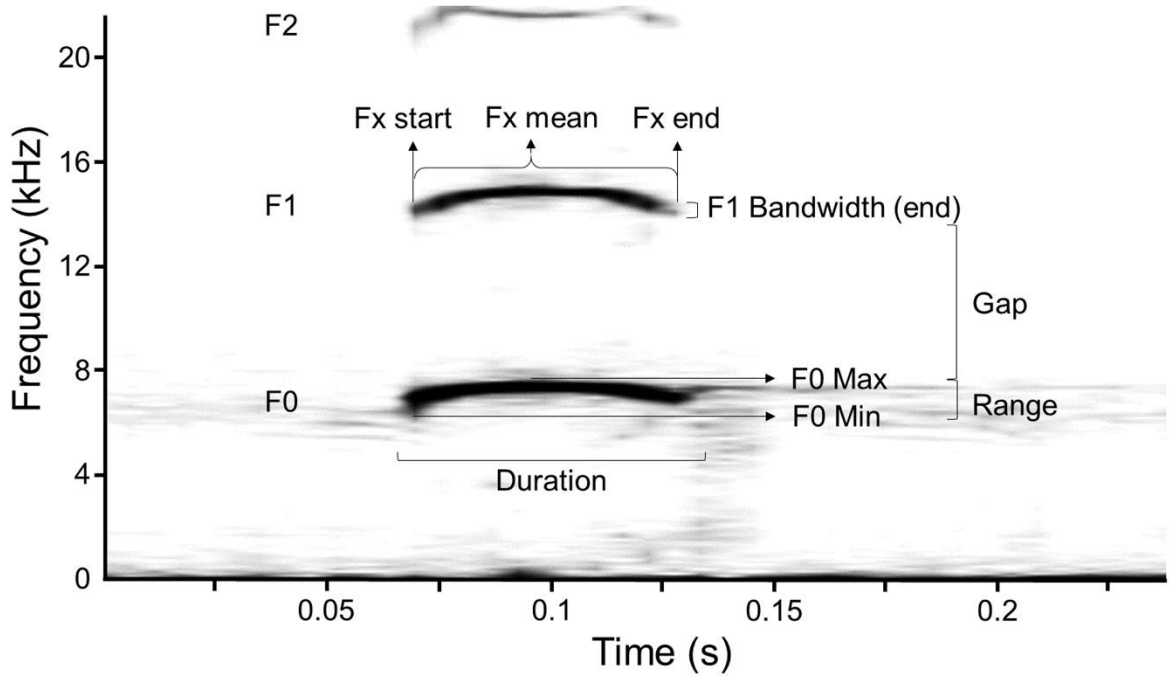

Figure 2.2: Dwarf mongoose recruitment call depicting a few basic parameters measured. These are the fundamental frequency band (F0), first formant (F1), second formant (F2), duration, overall minimum (F0 min) and maximum (F0 max) of the fundamental, range of the fundamental, frequency range between F0 and F1 (gap) and the bandwidth of the first formant, measured at the end of the call. All frequency measurements (Fx) such as mean, maximum, minimum and peak frequencies are measured at the start, mean and end of the frequency band.

To assess whether an individual's call rate was influenced by arousal/urgency, we examined sequences of isolation calls from seven individuals, and sequences of snake calls from nine individuals, from unedited field recordings. For each call type, we documented the number of

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calls the individual gave during the 30 s period immediately following the first recorded call, and the number it gave during the 30 s period after 1.5 minutes had elapsed since the first call. Within each call type, we compared these initial and subsequent call rates using paired t-tests.

Statistical analysis:

To identify the structural acoustic difference between recruitment calls elicited by snake encounters versus isolated individuals, we chose calls from individuals for which there were at least 5 good quality exemplars of both call types. This resulted in a sample of 683 calls (236 snake & 447 isolation) from 16 individuals. We first converted the data from the chosen parameters into principal components to eliminate the high levels of correlation between variables. The first five principal components (with eigenvalues above 1, Table 2.1) explained 88.947% of the variation and were then entered into a crossed permutation discriminant function analysis (pDFA: Mundry & Sommer, 2007) with 1000 permutations. This was performed in R version 3.2.3 (R Core Team, 2015) using the pDFA function by Roger Mundry, which is based on the Ida function of the R package MASS (Venables & Ripley, 2002). We tested statistical significance using a multivariate analysis of variance (MANOVA) in STATISTICA 13.

Table 2.1: Principal Components with eigenvalues >1, based on the 28 parameter variables of recruitment calls

	Eigenvalues	Cumulative Variance (%)
Principal Component 1	16.963	60.581
Principal Component 2	3.290	72.330
Principal Component 3	2.315	80.599
Principal Component 4	1.256	85.084
Principal Component 5	1.082	88.947

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2.3.3 Playback experiments:

To discern whether dwarf mongooses respond differently to the two types of recruitment call, we prepared tracks for 11 playback experiments. For each playback we randomly chose four good quality, monosyllabic exemplars of both snake and isolation calls from a single caller. We edited the calls in Adobe Audition 2.0 to remove excess background noise and equalised their volumes using Avisoft SASLab Lite (version 5.2.09). We then created a new isolation call track (and a new snake call track) by adding the four calls, in random order, with a 1.5 second interval between each call. This call-interval falls within the natural range for both snake (range 42-196 ms, *N*=56) and isolation (range 40-400 ms, *N*=58) calls. We then repeated this sequence eight times, resulting in a total of 32 calls per track. Finally, we added a minute of silence to either end of each track to allow for the monitoring of the target mongooses pre- and post-playback.

For each experiment we played recordings of snake and isolation calls from the same caller, thus avoiding any confounding effects of caller identity. The snake and isolation track from each of the 11 mongooses chosen as callers were played only once, to a randomly chosen non-alpha adult from the same group as the caller (4 male and 7 female targets from 4 groups). We separated the playback of the snake and isolation tracks by at least 30 minutes (average 40 minutes) and randomised the order in which they were played. We observed the target mongoose until it was foraging beyond the visual and auditory ('close' contact call) range of the original caller (to avoid any violation of expectations; Townsend, Allen & Manser, 2011). We then set up a speaker (Aiwa active speaker system model SC-A47; Sony Corporation, Japan) five meters from the foraging target mongoose, placing it behind vegetation so the target could not see it. We played calls with the Marantz professional portable recorder (model PMD-670). Call amplitude was set to 65 dB, measured with a handheld Velleman sound level meter (model DVM805; range 30-100 dB; 1.5 dB accuracy; Velleman, Belgium). This volume closely approximates the average amplitude measured for both isolation and snake recruitment calls. We recorded all playback experiments using a Sony Handycam (model DCR-SX60E; Sony Corporation, Japan) video recorder, monitoring the target mongoose for a

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range of potential responses. These included: latency to respond after the first call, duration of vigilance (alert scanning of the environment, with no foraging or social interactions), presence or absence of behaviours such as head-bobbing, creeping (alert advancing with belly close to the ground) or searching, the direction in which the target looked when searching and the distance of closest approach to the speaker. A targeted approach toward the speaker was distinguished from an incidental approach while foraging, by the presence of vigilant behaviour directed towards the speaker.

We paused experiments when they were interrupted before or between the playback of the first and second set of calls, and halted them entirely if the interruption occurred during an actual playback track. Potential interruptions included group movement to a different location, alarm calls, overhead helicopters, or other external factors causing disruption to normal foraging behaviour. Playbacks that were paused were resumed 10 or more minutes after the group had settled down again. Aborted experiments were performed again after at least six days had elapsed, to prevent negative habituation to the specific playback calls. To prevent the mongooses becoming habituated to recruitment call playbacks or the experimental protocol, we allowed at least three days to elapse (average 4.7 days) before conducting another playback experiment in the same group. Each caller-target pair was used only once.

Statistical analysis:

We conducted statistical tests in IBM SPSS v23 and STATISTICA v13 with an alpha level of 0.5. Where data sets were not normally distributed, we used nonparametric tests. To determine whether the playback of recruitment calls caused the target mongoose to change its behaviour, we compared (using Wilcoxon matched-pair tests) the time it spent vigilant during the 30 s period immediately prior to, and that immediately after, the first call in the playback track. We did this for both call types. To identify the specific effect of each type of call on the response behaviour of the target dwarf mongooses, we analysed playbacks using repeated measures (per individual) generalized linear mixed models (GLMM). Separate models were created for each of the three response variables a) response latency, b) duration

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of vigilance and c) closest distance approached. We tested each response variable with a Poisson log link distribution against the same set of fixed and random variables. Fixed effects were the primary predictor variable: context of call (snake vs isolation), order in which the tracks were played (treatment 1 vs 2) and the sex relation between the caller-target pair (same vs opposite sex). We included the identity of the target and the group to which it belonged as a random variable in all models.

2.4 Results

2.4.1 Sound analysis:

A crossed pDFA of isolation and snake recruitment calls confirmed that the two could be distinguished with high accuracy: 86.98% of selected calls were correctly classified and 86.19% correctly cross classified. The difference between the acoustic structure of call types was significant (MANOVA: $F_{5, 677}$=12.124, P<0.0001). The factors that loaded highest in the principal components were the entropy variables, duration and bandwidth of the fundamental frequency and the maximum frequency of both F0 and F1. Snake recruitment calls tended to be longer with a higher mean entropy and slightly lower fundamental and formant frequencies (Table 2.2). These parameters are thus probable cues on which dwarf mongooses base their response, whereas the remaining parameters may be common to recruitment calls.

Urgency (also termed arousal) appeared to influence the inter-call interval of recruitment vocalisations. The rate of an individual's isolation calls increased with time isolated, rising an average of 0.083 calls/s from the start of isolation to 1.5 minutes later (T-test for dependent samples: N=7, T=-5.05, P=0.002). In contrast, the rate of snake calls was higher, by an average of 0.367 calls/s, immediately after encountering a snake than 1.5 minutes later (T-test for dependent samples: N=9, T=3.811, P=0.005).

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Table 2.2: Mean ± SE of the acoustic variables which loaded highest for the principal components analysis of recruitment calls recorded in snake and isolation contexts

Acoustic Variables	Snake calls	Isolation calls
F0 Duration	147.11±5.542	72.69±0.866
F0 Mean f (at max)	7389.14±27.886	7569.79±31.504
F0 Median f (at max)	7414.85±28.472	7585.61±31.546
F0 Maximum f	7404.97±27.850	7582.78±31.567
F0 Entropy (mean)	215.52±0.142	213.82±0.124
F0 Entropy (median)	215.84±0.152	213.94±0.131
F0 Entropy (at start)	215.28±0.073	216.49±0.093
F0 Bandwidth (mean)	1214.13±23.214	1401.21±18.807
F1 Mean f (at max)	14717.08±56.253	15009.73±61.752
F1 Median f (at max)	14746.36±56.187	15068.46±62.192
F1 Maximum f	14721.94±56.269	15027.93±61.87

2.4.2 Playback experiments:

All recruitment calls influenced dwarf mongoose behaviour, with target mongooses increasing the time spent vigilant after hearing both snake (Wilcoxon matched-pairs test: T=0.00, Z=2.934, N=11, P=0.003) and isolation calls (Wilcoxon matched-pairs test: T=0.00, Z=2.803, N=10, P=0.005). Both call types were successful in recruiting target mongooses albeit to different extents. When hearing isolation calls, 27% of mongooses approached the speaker, whereas 91% approached during snake calls. Target mongooses remained vigilant for a longer period of time and approached the speaker more closely when hearing snake recruitment vocalisations than during isolation calls (Fig. 2.3; Table 2.3). Although the mean speed of initial response was faster towards snake than isolation calls, the effect was not significant. Neither the playback order nor the caller-target sex relation had a significant impact on any of the three response variables, nor did the identity of the target's group.

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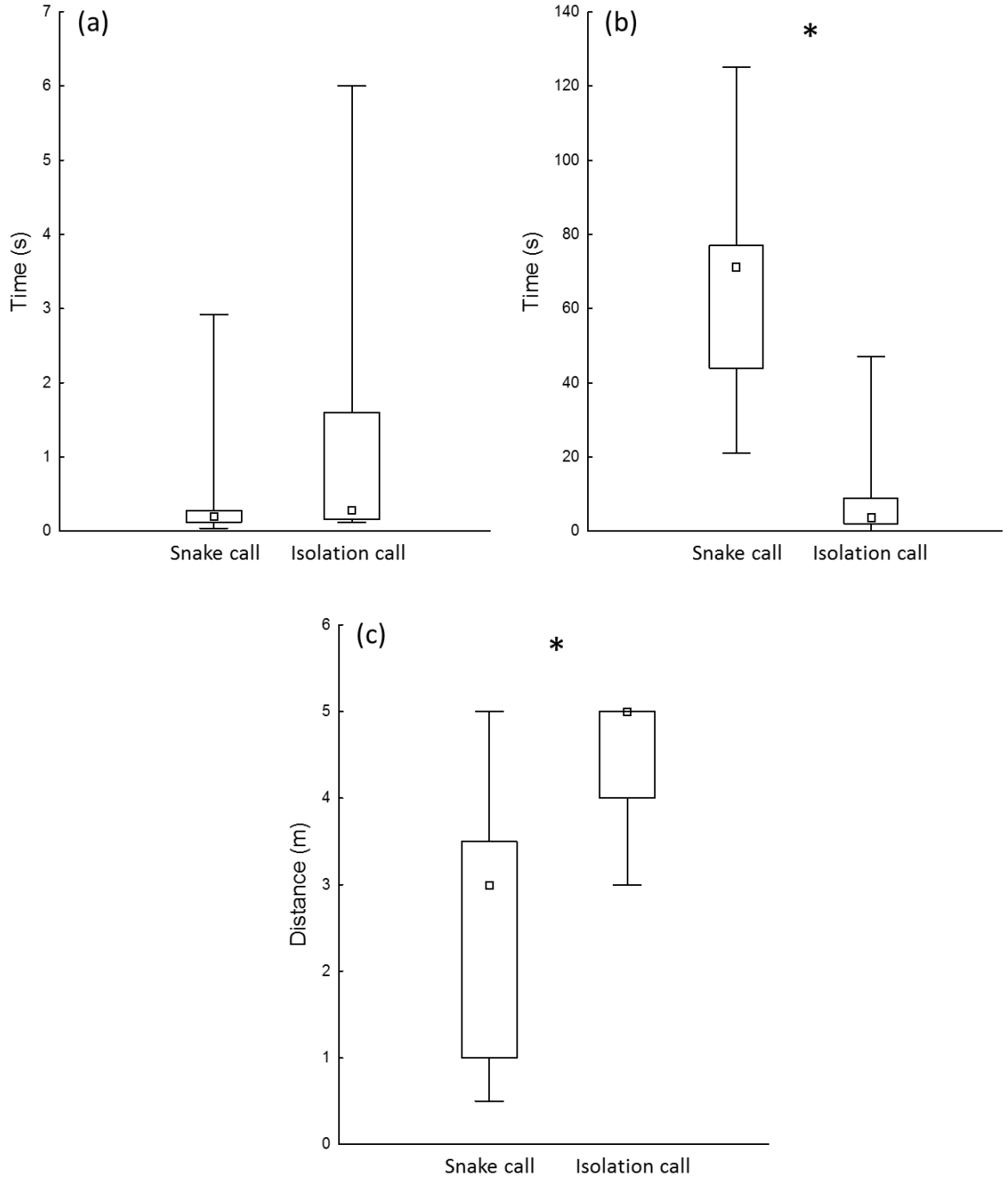

Figure 2.3: Median, quartiles and ranges of target mongoose: (a) response latency, (b) duration of vigilance and (c) closest distance obtained to the speaker during playbacks of snake and isolation recruitment calls. Context significantly influenced two of the three response variables (marked by asterisk) as shown in Table 2.3.

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Table 2.3: General linear mixed model results showing the influence of predictor (fixed effects) variables on the three response variables to dwarf mongoose recruitment playbacks

Predictor variable	*F*	*df*	*P*	*β*
a) Response Latency	3.012	3, 8	0.095	
Context (Isolation)	4.449	1, 11	0.059	3.541
Treatment order (First)	2.091	1, 7	0.190	1.167
Sex relation (Opposite sex)	2.173	1, 7	0.186	0.914
b) Vigilance Duration	7.665	3, 11	**0.005**	
Context (Isolation)	21.423	1, 12	**0.001**	-2.066
Treatment order (First)	0.083	1, 12	0.779	-0.090
Sex relation (Opposite sex)	1.147	1, 12	0.305	0.342
c) Closest Distance	2.756	3, 12	0.088	
Context (Isolation)	5.971	1, 12	**0.031**	0.364
Treatment order (First)	0.959	1, 13	0.345	0.115
Sex relation (Opposite sex)	0.733	1, 14	0.407	-0.103

Predictor variables each had two factors of which the first is displayed.

In addition to the shared recruitment function of these vocalisations, target mongooses displayed behaviours that were specific to each context. During the playback of isolation calls the dwarf mongooses looked only in the direction of the speaker (11/11 times), whereas during snake calls the target mongooses began searching nearby vegetation instead (11/11 times) and only occasionally looked towards the speaker (3/11 times). Target mongooses resumed foraging only after the final snake call had been heard but during the playback sequence for isolation calls. Finally, 100% of the responses to snake call playbacks included head bobbing and creeping; behaviours that were entirely absent during isolation call playbacks.

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2.5 Discussion

The calls emitted by dwarf mongooses to recruit group members to snakes or isolated group members may sound identical to a human observer but differ markedly from the perspective of dwarf mongooses. The differences in the acoustic structure of these two recruitment calls was sufficient to allow them to be accurately classified by context. Snake calls tended to be longer in duration, with a higher mean entropy, narrower bandwidth and lower F0 and F1 frequencies at maximum, than isolation calls. The playback experiments demonstrated that dwarf mongooses used these acoustic cues to tailor their response. Although both forms of recruitment call served to attract group members, snake calls were more effective than isolation calls. Additionally, target mongooses remained vigilant for longer after hearing snake recruitment calls. However, the mongooses also exhibited behavioural responses that were unique to call context. Upon hearing the playback of snake calls, the mongooses looked first for the potential threat, searching nearby vegetation and/or beneath rocks, presumably for the snake. In contrast, mongooses hearing isolation call playbacks looked in the direction of the caller (i.e. the speaker). Mongooses also responded to snake call playbacks with head-bobbing (to gain better visual perspective) and creeping (i.e. approaching with extreme caution); behaviours never observed during isolation call playbacks. Searching the ground in response to snake warning calls has also been documented for vervet monkeys (Seyfarth, Cheney & Marler, 1980) and Japanese great tits, *Parus major minor*, (Suzuki, 2012). Similarly, head-bobbing in response to warning calls or visual threats has been described in a range of species, including meerkats (Graw & Manser, 2007), black-winged stilts, *Himantopus himantopus,* (Goriup, 1982) and Mexican free-tailed bats, *Tadarida brasiliensis,* (Bohn, Schmidt-French, Ma & Pollak, 2008). The finding that dwarf mongooses exhibit unique, appropriate and consistent differences in their response to recruitment calls derived from these two contexts confirms that receivers perceive these recruitment calls as distinct, functionally referential signals. Whether the recruitment calls used by this species in other contexts are also context-specific can be ascertained only by further research.

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Although we cannot entirely discount the possibility that the acoustic differences between isolation and snake calls stemmed from differences in the arousal of the caller (reflecting context-specific differences in risk), the two calls were consistently distinctive and did not grade into one another as would be anticipated if their structural differences were urgency-based. Graded calls would have less distinguished acoustic differences and thus have a low percentage of accurate classification. As in many other species (Naguib et al., 1999; Warkentin, Keeley & Hare, 2001; Ellis, 2008; Scheumann et al., 2012; Manser et al., 2014; Gersick et al., 2015), urgency in dwarf mongoose recruitment calls appeared to be conveyed by call rate, with inter-call interval decreasing with increasing threat/arousal. Lost mongooses (who typically ran around their territory searching for their group) increased their call rate as their time alone increased and they became visibly more agitated. Similarly, mongooses that discovered a potentially lethal snake showed a high initial call rate, when risk/urgency was at its greatest. Call rate then decreased over time as the threat was pinpointed, investigated and conspecific support arrived. Qualitative observations suggest that call amplitude was also positively correlated with urgency in both the recruitment and alarm calls of dwarf mongooses (Sharpe, personal observation), as is the case in many birds and mammals (Briefer et al., 2012; Suzuki, 2016). However, both the rate and amplitude of calls were controlled in the playback experiments so these indicators of urgency could not have influenced the target mongooses' responses. Call duration is another parameter that commonly varies with caller arousal and context urgency (Briefer et al., 2012; Suzuki, 2016). In birds, call length typically decreases with increasing urgency (Suzuki, 2016) but in mammals the relationship is less clear (reviewed in Briefer et al., 2012). However, for both meerkats (Manser, 2001) and dwarf mongooses (Beynon & Rasa, 1989) alarm call duration decreases in high urgency situations. For example, the 'panic twitters' of dwarf mongooses become 25% shorter when a predator is presented at a distance of 5 m as compared with 10 m (Beynon & Rasa, 1989). Given this, it is unlikely that the target mongooses in our experiments were using call duration to determine the degree of threat: snake calls were longer than isolation calls yet they elicited a stronger, more urgent response.

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For a vocal signal to be functionally referential it must have production and perception specificity (Macedonia & Evans, 1993; Townsend & Manser, 2013; Suzuki, 2016); i.e. the call must be distinctive to context, both acoustically and by the response it elicits. The unique, qualitative differences in the mongooses' response to the calls show that they perceive the calls as functionally referential, and it is highly probable that the requirements of production specificity are also met.

Our findings raise the question of why dwarf mongooses evolved a distinct, functionally referential recruitment signal, for cooperative snake mobbing in particular, when their close relatives – banded mongooses and meerkats – use a graded, urgency-based recruitment system (Manser, 2001; Manser et al., 2001a; Furrer & Manser, 2009a). Such disparity between closely related species is not unusual; for example, the food-associated calls of chimpanzees are graded and arousal-based while those of bonobos (*Pan paniscus*) are functionally referential (Clay & Zuberbühler, 2009). It has been argued that discrete, functionally referential calls evolve when receivers need precise information about context in order to choose the most adaptive response (Manser et al., 2014). For example, species threatened by predators that use multiple hunting strategies and which live in complex habitats (that provide more than one means of escape) will greatly benefit from alarm calls that provide explicit information that allows them to adopt the safest escape strategy (Macedonia & Evans, 1993). However, attempts to identify ecological or social factors (such as habitat complexity or social complexity) that predict the occurrence of functionally referential signals across taxa have not been successful (Furrer & Manser, 2009b).

It appears unlikely that differences in ecology or social complexity led to the evolution of functionally referential recruitment calls in dwarf mongooses but not meerkats and banded mongooses. Although dwarf mongooses may be more vulnerable to snakes (being smaller and having smaller social groups; Manser et al., 2014), all three species are threatened by large snakes and exhibit very similar snake-mobbing behaviours (Graw & Manser, 2007;

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Furrer & Manser, 2009b; Kern & Radford, 2016). The cause appears to be related to interspecies differences in the signalling systems used for recruitment. The suite of contexts that elicit recruitment calls in banded mongooses and meerkats (snakes, secondary predator cues and intergroup encounters) all require the group to respond with cautious investigation (Graw & Manser, 2007; Müller & Manser, 2007; Furrer & Manser, 2009b). These calls appear to signal the presence of a potential threat that requires group inspection, rather than simply a 'come hither' message. As a consequence, urgency-based acoustic differences in the recruitment call (and a simple strengthening of response by receivers) is sufficient to elicit an appropriately wary response. In contrast, dwarf mongoose recruitment calls do not appear to warn of danger and serve to merely attract group members. The other contexts in which they are used (isolation, mate attraction and group retreat) pose no direct threat to receivers and do not require wary investigation. Secondary predator cues do not elicit vocalisations in dwarf mongooses (Morris-Drake, Kern & Radford, 2016) and this species uses 'leading' contact calls when initiating potentially risky inter-group encounters (Sharpe, personal observation). Under these circumstances, dwarf mongooses would benefit greatly from developing a functionally referential snake recruitment call to ensure that group members respond with appropriate caution.

In conclusion, this study is the first to compare recruitment vocalisations from widely disparate contexts (isolation and cooperative defence), and to demonstrate that they are functionally referential. The acoustic indicators of context contained within this species' recruitment calls not only allow group members to immediately adopt the most appropriate behavioural response (as has been demonstrated with functionally referential alarm calls; Manser et al., 2001b), but they also provide individuals with the information they need to decide whether to respond at all (i.e. whether to contribute to the group's cooperative activities). We would predict that other social species that use their recruitment calls in multiple and diverse contexts will also produce context-specific recruitment signals.

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Chapter 3:

Dwarf mongooses use sex and identity cues in isolation calls to discriminate between callers

(Accepted by *Animal Behaviour* for publication)

3.1 Abstract

The information transmitted by acoustic signals has attracted much scientific interest in recent years. However isolation calls, which are long-distance vocalisations used by lost group members to reunite with their social group, have been surprisingly neglected. These calls assist in maintaining group cohesion and are thus particularly important in species that depend on the group for survival or reproduction such as cooperative-breeders. Our study therefore examined the information transmitted by the isolation vocalisation in a wild cooperatively-breeding carnivore: the dwarf mongoose (*Helogale parvula*). We ran acoustic analysis for informative cues within isolation calls, and conducted a series of playback experiments to identify whether mongooses were capable of discriminating between callers based on these cues. The acoustic structure of dwarf mongoose isolation vocalisations contained information concerning the caller's identity, sex and potentially also group-membership. Target mongooses were able to discriminate between own-group and extra-group callers and biased their response based on the sex of the caller. They responded more quickly and for a longer period of time, and approached more closely for calls of foreign females than calls of female group-mates. This is the first time that sex-specificity has been demonstrated in the

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vocalisation of an Herpestid, and we suggest that dwarf mongooses eavesdrop on the calls of isolated foreigners and may use isolation calls to attract and identify potential mates.

3.2 Introduction

Over the past few years studies on animal vocalisations have burgeoned, and the information transmitted by acoustic signals is more widely understood (Taylor & Reby, 2010). There are, however, still many areas of acoustic communication that are poorly studied. One such vocalisation is the isolation call which is found in many mammalian species. These calls (also called lost, separation or distress calls) are characterised by their high frequency and pure tone traits. Such traits transmit well in 'noisy' and densely vegetated environments and appear to be perceived as more 'fearful' and less aggressive than harsher tones (Morton, 1977; Scheumann, Zimmermann & Deichsel, 2007; Manser et al., 2014). The isolation call is a long-distance recruitment call that facilitates a lost group member to reunite with its group. It is thus fundamentally important in maintaining group-cohesion in social species (Digweed, Fedigan & Rendall, 2007).

It is important for long-distance calls in particular to contain discernible information about context or identity, so that receivers are able to perform the appropriate response rapidly, in the absence of additional cues (Gersick, Cheney, Schneider, Seyfarth & Holekamp, 2015). Despite this importance, the majority of studies focus on only the calls of isolated infants (Gelfand & McCracken, 1986; Balcombe, 1990; Scherrer & Wilkinson, 1993; Weary, Lawson & Thompson, 1996; Brudzynski, Kehoe & Callahan, 1999; Monticelli, Tokumaru & Ades, 2004; Bohn et al., 2007; Knörnschild, von Helversen & Mayer, 2007; Knörnschild, Nagy, Metz, Mayer & von Helversen, 2012; Scheumann, et al., 2007; Scheumann, et al., 2012; Schneider & Fritzsche, 2011). Studies on isolation calls in adult mammals on the other hand, are rare, concentrating almost exclusively on primates. These primate calls commonly inform audience members about the individuality, sex, age, group or family membership and context of the call.

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For example, the isolation call (or combination long call) of cottontop tamarins, *Saguinus oedipus*, is specific to the sex of the caller and individuals respond favourably to the parameter traits of calls of the opposite sex (Miller, Scarl & Hauser, 2004). The calls of white-faced capuchins, *Cebus capucinus,* differ between individuals, with group members responding most commonly to individuals of the highest rank (Digweed et al., 2007). Squirrel monkey, *Saimiri sciureus*, calls are individually distinct across all ages (Lieblich, Symmes, Newman & Shapiro, 1980) and in chacma baboons, *Papio cynocephalus ursinus*, calls not only differ between individuals, but also provide an indication of the context in which they are produced (Fischer, Hammerschmidt, Cheney & Seyfarth, 2001, 2002). In the latter two species however, studies did not explore whether individuals are capable of recognising and responding to these acoustic cues.

Little is known about non-primate adult isolation vocalisations and the information they transmit. One study on Amazonian manatees, *Trichechus inunguis*, found individual, sex and age differences, though the recognition of individuals by manatees was tested only with preliminary playback analyses (Sousa-Lima, Paglia & Fonseca, 2002). In other mammals, such as giant otters, *Pteronura brasiliensis* (Mumm & Knörnschild, 2014), isolation vocalisations have only been recorded and/or described but not examined for the information they convey to conspecifics.

Our study examines the information transmitted by the isolation calls of a wild cooperatively breeding mammal: the dwarf mongoose (*Helogale parvula*). Isolation calls are of special significance to cooperative species because individuals generally cannot survive or breed except within a group, and large group size is associated with many benefits. In dwarf mongooses and meerkats, both juvenile and adult survival increases with group size. This is because larger packs are more able to defend themselves against predation and territorial incursions, and can raise more pups due to the higher number of helpers contributing to baby-sitting, feeding and protecting the young (Rood, 1986; Clutton-Brock et al., 1999). Separation from the group is costly and exposes individuals to high levels of predation and stress (e.g.

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Young & Monfort, 2009). Surprisingly though there is only one study - that of cottontop tamarins (Miller et al., 2004) - which has investigated isolation calls in cooperative mammals.

Dwarf mongooses are an ideal study species in which to investigate isolation calls. They live in stable social groups of up to 30 individuals of which females are the philopatric sex. They can be found in wooded savannah regions of Africa, taking refuge in termite mounds by night and foraging as a dispersed group by day (Rood, 1990; Sharpe, Joustra & Cherry, 2010; Manser et al., 2014). Foraging group members maintain contact using individually recognisable contact calls (Sharpe, Hill & Cherry, 2013) but when an individual becomes inadvertently separated from the group it produces monosyllabic, high-pitched isolation calls to facilitate their reunion. We undertook acoustic analysis and playback experiments to determine what information - such as identity, sex and group-membership - is contained within dwarf mongoose isolation calls and whether individuals were capable of recognising and responding to these acoustic cues.

3.3 Methods

3.3.1 Sound recording:

We recorded the isolation recruitment calls of dwarf mongooses that had become separated naturally from their group, between March 2015 and March 2016. Calls were collected from 40 mongooses across four wild groups (mean group size 16) at Phuza Moya Private Game Reserve (coordinates: 24°16’10’’S, 30°47’46’’E), in Limpopo, South Africa. See Sharpe et al. (2010) for details on climate and vegetation. Each individual in the study population was marked for recognition using small spots of blonde hair dye, applied with a long-handled paintbrush while the animal was sunning. Mongooses less than 9 months old were excluded from the study. This population has been studied since 2006 and the mongooses were habituated to close observation, allowing us to record calls within three meters. Vocalisations were captured using a Marantz PMD-670 solid state recorder and a Roland R26 portable

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recorder, both attached to Sennheiser directional microphones (model ME66/K6) with windshields. We recorded calls opportunistically during the mongooses' morning foraging period by following the mongoose group on foot and finding the separated caller when isolation calls were heard. The close proximity to the study subject allowed for positive identification of both the caller and the context. However, since the distance from the callers was not constant and background noises could not be controlled, the amplitude (volume) of individual recordings and isolation calls varied. We terminated recordings if wind speeds were greater than 11 km/h or if cicadas began calling, as their call frequency overlapped with that of the mongoose isolation calls (Fig. 3.1d). We performed spot checks using a Velleman sound level meter (model DVM805; range 30-100 dB; 1.5 dB accuracy) to obtain calling amplitudes for playback and standardisation purposes.

We digitised (wav format, 48 kHz, 16 bit) and edited recordings for playback and analysis using Adobe Audition 2.0. Out of the 1407 calls isolated from recordings, 875 were from known callers and were of sufficient quality to be used in analysis, resulting in a sample of 40 mongooses. Due to the rarity of these calls, and therefore small sample size per individual, all available calls of sufficient quality were analysed. We deemed calls to be of high quality if they had a high signal to noise ratio, did not overlap, had little background interference (such as wind, cicadas, birds or flies) and at least the first formant above the fundamental frequency band was clearly visible (Fig. 3.1). The calls of younger mongooses were often too high for the second formant to be within recorded frequencies. Therefore only the fundamental and first formant frequency bands were considered. We constructed spectrograms for visualisation of vocalisations in Raven Lite 1.0 (50% brightness, 60% contrast and spectrogram sharpness 512 pts).

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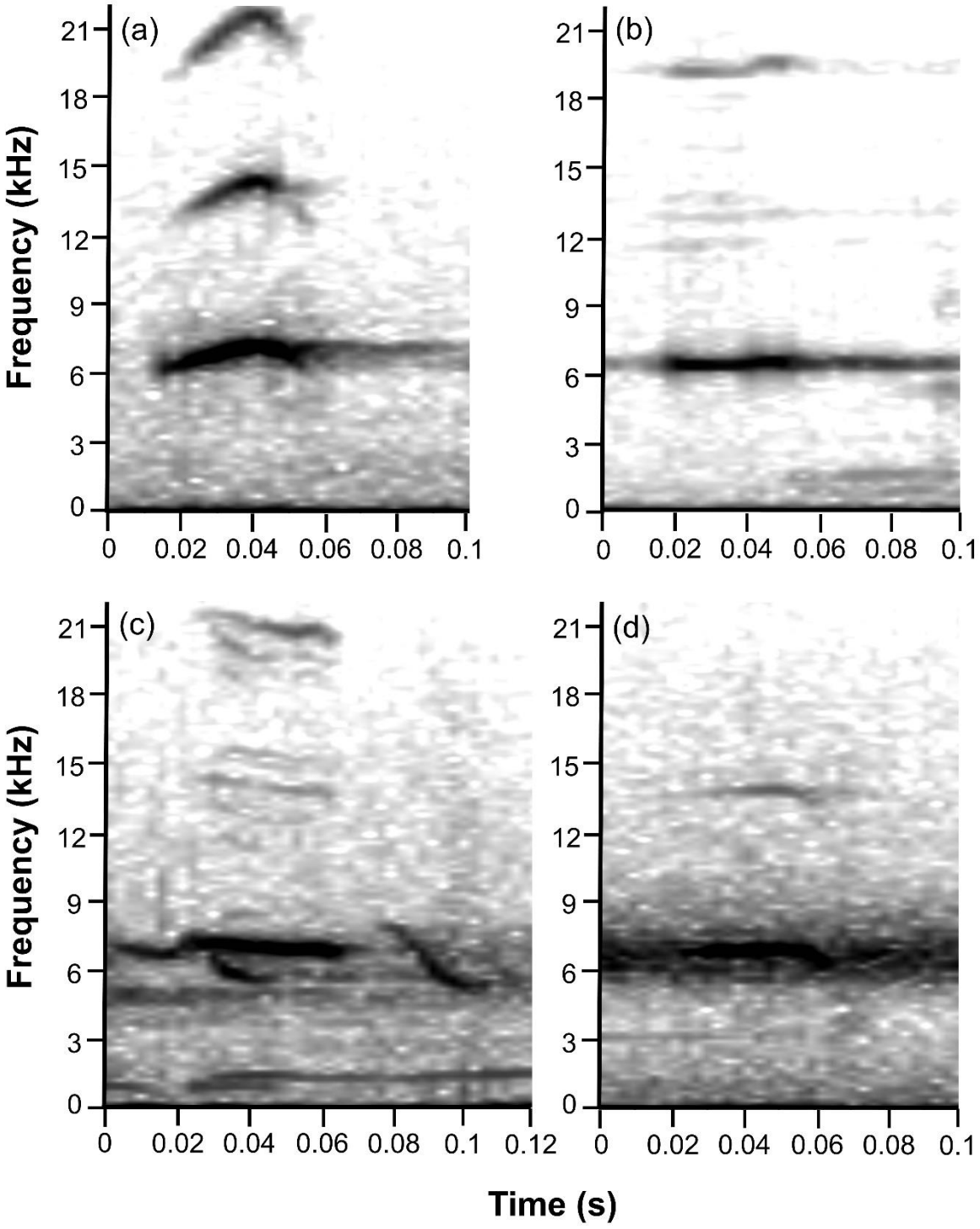

Figure 3.1: Spectrographic examples of good (a) and bad (b-d) quality calls from an adult male mongoose (HM048). Bad quality calls include those that: (b) have one or more poorly visible formants, (c) are obscured by other sounds such as bird calls and (d) where the fundamental frequency is entirely obscured by cicada chirps.

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3.3.2 Sound analysis:

To examine isolation calls for potential informative characteristics, we used Luscinia bioacoustics software (RF Lachlan version 2.0) and analysed all possible acoustic parameters of 875 calls, for both formants (F0 & F1), by Fast Fourier Transformation (1024 points, Hamming Window, time step 0.36 ms, frame length 23.22 ms, spectral overlap 98.45%). One advantage of this software is that for each individual call, the frequency bands of interest must be highlighted manually, increasing accuracy of measurements particularly as background noise can confuse automated measures (Baker & Logue, 2003). We analysed temporal and spectral parameters with all frequency-related variables being measured at the mean, median, maximum, minimum, time of maximum, time of minimum, start and end of each call. We chose 20 of the most commonly used parameters for statistical analysis of isolation calls. For both the fundamental (F0) and first formant (F1) frequency bands, the following parameters were measured: overall peak, minimum and maximum frequency; peak frequency (at mean); and mean frequency (at mean and max). In addition, we measured the duration, power spectrum quartiles, Wiener entropy, bandwidth (at mean and max) and range of the fundamental frequency. Finally we calculated the gap, or formant dispersion, between the two frequency bands (mean F1-F0).

Although parameters were measured for all calls of sufficient quality, only calls from those individuals with more than six exemplars were used for statistical analysis (*N*=784 calls from 28 individuals, mean 28 and range 6-115 calls per individual). Furthermore, one mongoose female was excluded from the statistical analysis because her calls were on average 2249 Hz lower than those of the other mongooses (Fig. 3.2).

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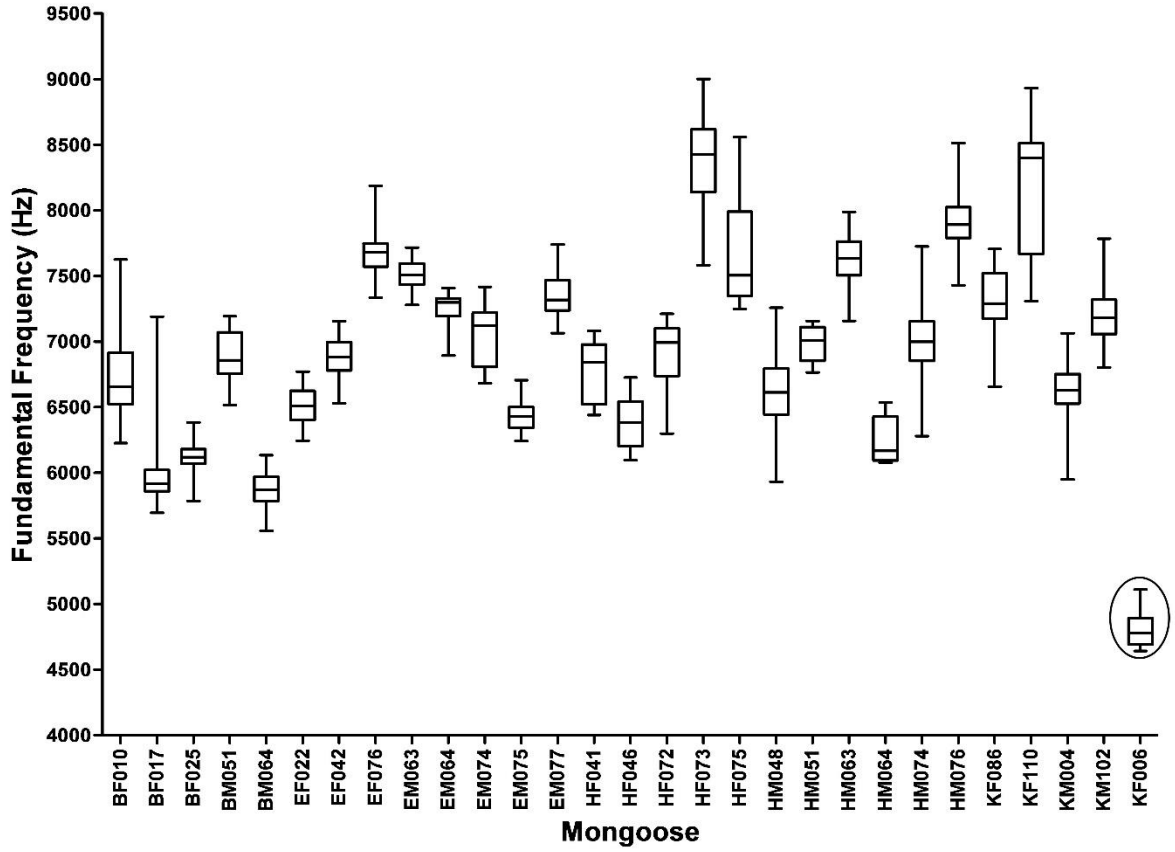

Figure 3.2: The fundamental frequency range, percentiles and medians of the isolation calls of all dwarf mongooses. Analysis included 5 mongooses from the group Bugbears, 8 from Ecthelion, 11 from Halcyon and 4 from Koppiekats. Note the excluded outlier KF006 (circled). For each caller, the name code denotes group membership (B, E, H or K), followed by sex (M or F) and number by birth or immigration within the group.

Statistical analysis:

We ran a series of statistical tests to determine whether the acoustic structure of isolation calls conveys information concerning identity, sex and group membership of the caller. First, we ran a principal components analysis (PCA 1) for the 20 chosen acoustic parameters (using mean of calls per caller) to eliminate the high levels of correlation between variables. The PCA with varimax rotation yielded three components with eigenvalues >1, which accounted for 98.052% of the variation (KMO>0.5; Bartlett's X^2_{190}=2155.19, P<0.0001). We used the scores of these principal components to perform one-way multivariate analyses of variance

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(MANOVA) and stepwise discriminant function analyses (DFA) with leave-one-out cross-validation to identify whether callers could be classified according to a) group and/or b) sex. Post-hoc analyses of variance then enabled us to identify: first, which groups differ from one another and how; and second, which principal components differ significantly for groups and for sexes and therefore the acoustic parameters which may be important for recognition. Furthermore, because females are the philopatric sex in dwarf mongooses and the presence of immigrant males within a group could potentially confound results, we re-tested group distinction with a stepwise DFA and MANOVA using only female callers. Finally we calculated principal components for call data (PCA 2), including every available call per individual (KMO>0.5; Bartlett's X^2_{190}=52740.303, P<0.0001). We then entered the scores of the first two components (89.258% variation) into a stepwise DFA and MANOVA to determine whether isolation calls are also individually specific. We also tested individuality within each group separately. We performed all statistics in IBM SPSS statistics v23, and for each DFA we adjusted prior probabilities by the unequal group sizes.

3.3.3 Playback experiments:

To test whether dwarf mongooses were capable of utilising acoustic cues and distinguishing between calls of familiar and foreign individuals, we devised playback experiments. We prepared 160 randomly chosen distinct isolation calls from 30 non-alpha adult mongooses as stimuli for the playback experiments. Once extracted, calls were prepared by removing background noise with Adobe Audition 2.0 and equalizing call amplitude in Avisoft SASLab Lite (version 5.2.09). We used the Adobe Audition fade in and out functions to minimize the impact of residual background noise between calls. All tracks for playback consisted of four distinct isolation calls (exemplars) from a single caller, repeated eight times (32 calls total) with two second intervals between each call. This inter-call interval falls within the natural range (N=58 call sequences). We added a minute of silence to either end of each track for observation of mongoose behaviour before and after each playback.

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For the playback procedure we played recordings of isolation calls from two different callers (separated by at least thirty minutes) to a target mongoose. The callers consisted of an own-group member and a mongoose from another group (referred to as 'foreign'), paired by sex, dominance status and age to avoid any potential confounding effects of class-specific signatures. Although the most common protocol for testing vocal recognition takes the form of habituation-discrimination experiments, this method was not feasible for dwarf mongoose isolation calls. Playbacks of prolonged bouts of calling from a single caller caused the audience to become increasingly interested instead of habituating to the stimulus. Therefore calls from the two individuals were played separately, in random order (treatment Foreign-Own or Own-Foreign) for each experiment, and the behaviour of the target documented. Playback experiments were conducted on 20 randomly-chosen, non-alpha, adult target individuals from the four groups (five Bugbears, four Ecthelion, five Halcyon and six Koppiekats), of which 11 were female and nine male. The sex of the target was also chosen randomly, ensuring only that there were at least six target-caller pairs of the same sex and six of the opposite sex.

We conducted the playback experiments during summer (December 2015 to March 2016) on sunny, relatively windless (<11 km/h) days. Strong wind can impact playbacks as mongooses become nervous and the playback stimulus is not as clearly audible. A speaker (Aiwa active speaker system model SC-A47) and a Marantz professional portable recorder (model PMD-670) were set up 5 m from the target mongoose, and obscured from view by vegetation. We chose this distance because during the recording of playback stimulus it was observed that isolation vocalisations are often produced when the mongoose is obscured from but relatively close to its group, and during intergroup encounters both own-group and foreign mongooses may be in close proximity to the caller. We used natural markers such as sticks and stones to indicate meter intervals radiating from the speaker to facilitate later distance measurement. For each experiment a Velleman sound level meter (model DVM805) held 0.5 meters from the speaker was used to set the stimulus volume to 65 dB which falls within the natural range of dwarf mongoose recruitment calls (as measured by spot tests, N=18). We

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paused trials before the onset of calls if the target mongoose became obscured from view or if the group was disturbed by alarm calls, playing, group movement or sudden increased background noise (such as passing aircraft or strong gusts of wind). The playback was then resumed as soon as natural foraging behaviour recommenced. If however trials were interrupted during the playback of calls, we halted the experiment and re-ran it after at least one other experiment had been performed in the same group (minimum of 6 days between). To prevent habituation to the test stimulus and protocol, we used each exemplar in only one trial and used each trial and target mongoose only once. We allowed a minimum rest period of three days (average 11) between experiments within the same group. Finally, although it was sometimes necessary to use an individual caller twice (average usage 1.3 times), different exemplars were employed each time and in the opposite capacity (own or foreign caller) and were therefore heard by a different group.

We recorded the response of the target mongoose to both trials using a Sony Handycam (model DCR-SX60E) video recorder for the duration of each playback track. The camera was held at a distance of three meters from the mongoose with minimal movement of the observer to avoid disturbing the target individual and for ease of later analysis. For each experiment we noted the location within the territory of the experiment, group behaviour and identity of the target mongooses. Response was measured with frame-steps on the KMPlayer (version 2.9.3.1432) as: the latency to react from the first call of the playback sequence; the time until first movement towards the speaker; the amount of time spent vigilant; and the closest approach to the speaker. Vigilance was defined as a pause in foraging to scan the environment, look towards the speaker or more constantly survey the surroundings. We also noted the following behavioural responses: no visible response; first response; orientation towards the speaker; change of posture to obtain a different perspective (i.e. crouch or stretch the front elbows); adopt bipedal stance; perch on an object for elevation; or go on guard (constant vigilance from an elevated perch). Each behaviour was given a score of 1 if present and summed per playback recording.

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Statistical analysis:

To investigate the difference in responses to foreign and own group callers, we ran Wilcoxon matched-pairs tests by response variable for the 20 target mongooses. These tests were run separately by the sex of the caller (*N*=11 female and 9 male caller pairs) as the presence of male or female foreigners within their territory may influence dwarf mongooses differently. To ensure that target mongooses did not simply respond stronger to the first or the second playback, we ran a further Wilcoxon matched-pairs test with treatment order as the independent variable. Similarly we tested and compared the level of vigilance in the minute prior to each playback to ensure that potential differences in behavioural state did not influence the responses.

3.3.4 Ethical note:

The experimental procedures conform to South African laws and were approved by the ethics committee of Stellenbosch University (SU-ACUD16-00016). No dwarf mongooses were ever captured or otherwise handled and our experiments had no apparent after effects on the mongooses' behaviour. We observed no negative habituation (decrease or change in response) to natural isolation calls after playback experiments.

3.4 Results

3.4.1 Sound analysis:

Callers could be accurately assigned to group with 60.7% correct classification and 46.4% cross-validated correct classification. Group acoustics differed from one another (MANOVA: $F_{9,\ 53.693}$=2.272, *P*=0.031). However, a post-hoc Tukey HSD test showed that this difference lay only between two of the groups: Bugbears and Halcyon (*P*=0.032), whose territories were located furthest apart (Fig. 3.3).

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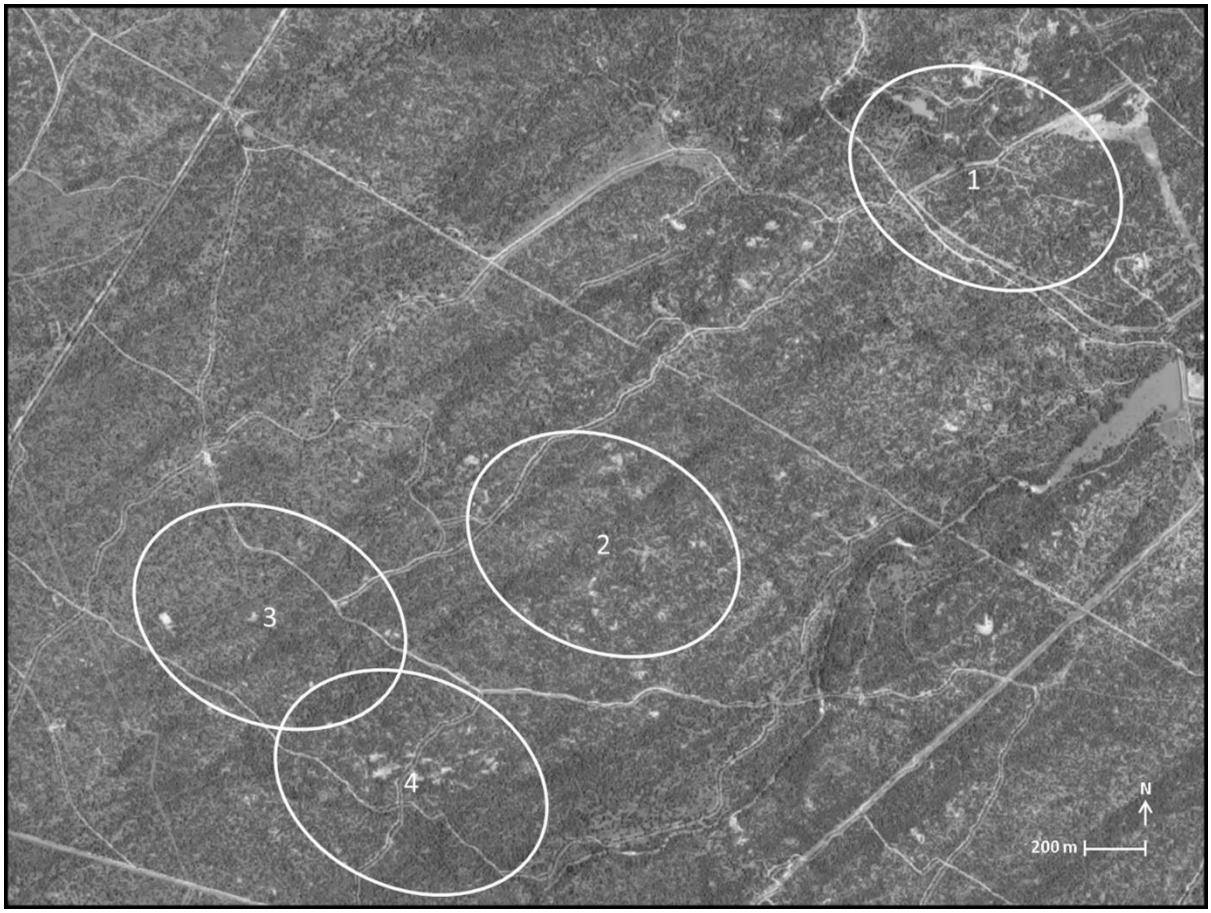

Figure 3.3: Map (adapted from google maps) of the approximate territories of the dwarf mongoose groups studied on Phuza Moya private game reserve: 1. Bugbears, 2. Koppiekats, 3. Ecthelion, 4. Halcyon.

Callers could also be accurately assigned to their sexes with 78.6% of cases and 71.4% of cross-validated cases correctly classified. The two sexes differed significantly in the acoustic structure of their isolation calls (MANOVA: $F_{3, 24}$=4.326, P=0.014).

The difference between groups lay within the first principal component (ANOVA: $F_{3,24}$=3.445, P=0.033) whereas that for sexes falls in the second principal component (ANOVA: $F_{1,26}$=14.044, P<0.001) as can be seen in Fig. 3.4. The parameters which loaded highest for these components (Table 3.1: PCA 1) and accounted for most of the variation are thus the acoustic cues which dwarf mongooses may utilise.

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When we tested the data for female mongooses in each group (i.e. known kin), we found no group signature in isolation vocalisations (DFA: 53.8% and 15.4% cross validated classification; MANOVA: $F_{9, 17.187}$=1.224, P=0.343).

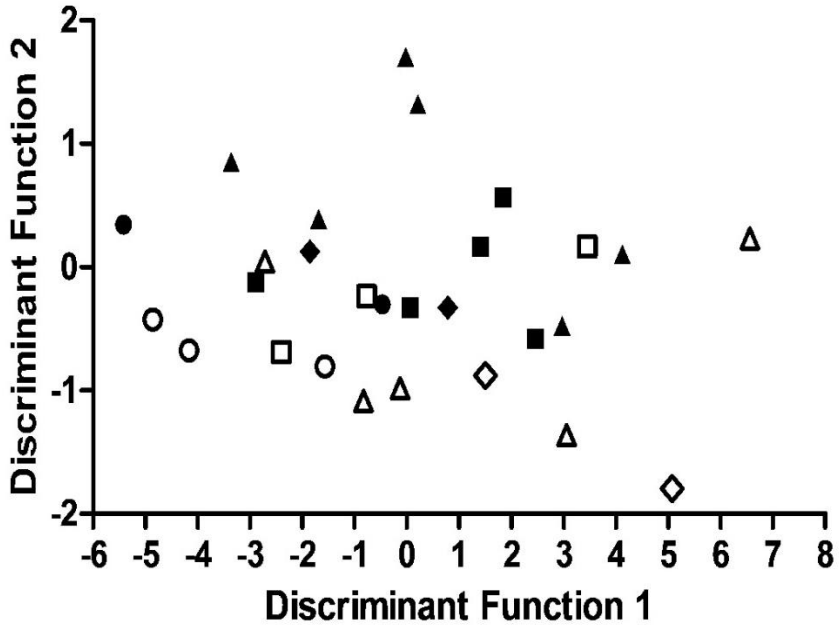

Figure 3.4: Signal space plot of the isolation calls of 28 dwarf mongooses based on the first two discriminant functions. Data points represent group centroids of individual callers. Groups differ by symbol (circle: Bugbears, square: Ecthelion, triangle: Koppiekats, diamond: Koppiekats) and sexes differ by shading (white: females, black: males). Note that DF1 was more important for group distinction and DF2 for distinction between sexes.

Finally, a stepwise discriminant function analysis with leave-one-out cross-validation on the principal components of the call data revealed that these recruitment calls were also individually specific with 43.8% of cases and 43.4% of cross-validated calls correctly assigned. Individuals differ significantly (MANOVA: $F_{54, 1510}$=79.251, P<0.0001). The factors that loaded highest into the principal components included the third quartile and mean peak frequencies of F0 and F1 (Table 3.1: PCA 2). The DFA results improved when the data was analysed per group (Table 3.2).

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Table 3.1: Factor loadings (>0.5) for each call parameter entered into each PCA

	PCA 1: Group & Sex			PCA 2: Individuality	
Parameters	PC 1	PC 2	PC 3	PC 1	PC 2
F0 PS Quartile 3	0.997			0.992	
F0 Mean f (max)	0.996			0.991	
F1 Peak f (mean)	0.995			0.990	
F1 Maximum f (overall)	0.995			0.988	
F1 Peak f (overall)	0.995			0.988	
F0 PS Quartile 1	0.995			0.986	
F0 Peak f (overall)	0.994			0.982	
F0 Peak f (mean)	0.994			0.981	
F1 Mean f (mean)	0.994			0.980	
Gap (F1mean-F0mean)	0.993			0.980	
F1 Mean f (max)	0.993			0.977	
F0 Mean f (mean)	0.990			0.976	
F0 Maximum f (overall)	0.989			0.966	
F1 Minimum f (overall)	0.955			0.861	
F0 Minimum f (overall)	0.852	0.507		0.712	0.646
F0 Range	0.717				-0.835
F0 Bandwidth (mean)		-0.897			-0.818
F0 Bandwidth (max)		-0.874		-0.543	0.784
F0 Entropy (mean)	-0.604	0.781			-0.649
F0 Duration			0.968		

Table 3.2: Discriminant function analysis and multivariate analysis of variance results for individual-specificity of isolation calls in each group of dwarf mongooses

	DFA		MANOVA		
Groups	stepwise DFA	Cross validation	*F*	*df*	*P*
Bugbears	68.0%	67.2%	32.675	8, 238	****
Ecthelion	65.0%	64.2%	51.501	14, 256	****
Halcyon	65.8%	63.5%	79.344	20, 672	****
Koppiekats	89.1%	86.2%	76.434	6, 338	****

**** P<0.0001

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3.4.2 Playback experiments:

Isolation calls successfully recruited dwarf mongooses, with target mongooses approaching the speaker for 65% of playbacks of foreign callers and for 30% of playbacks of own-group callers. Dwarf mongooses responded more strongly to playbacks of foreign callers than to playbacks of their own group members but only when the callers were female (Table 3.3; Fig. 3.5). They responded faster, moved closer, remained vigilant for a longer period of time and displayed more varied behavioural responses to foreign female calls. For familiar and foreign male callers all response variables did not differ (Table 3.3; Fig. 3.5).

Dwarf mongooses did not bias their responses based on the order of playbacks (Table 3.3), and there was no difference in the amounts of time they spent vigilant immediately before each treatment (Wilcoxon matched-pairs test: N=20, T=83, Z=0.821, P=0.411).

Table 3.3: Wilcoxon-matched pairs results of responses to male and female dwarf mongoose isolation calls when the playbacks were foreign vs own group members and first vs second treatment respectively

	Male callers				Female callers			
Own vs Foreign	*N*	*T*	*Z*	*P*	*N*	*T*	*Z*	*P*
First response	9	9.5	1.540	0.124	11	7	2.312	0.021
First step towards	5	1	1.753	0.080	7	0	2.366	0.018
Response duration	8	7	1.540	0.123	11	0	2.934	0.003
Closest distance	3	0	1.604	0.109	8	0	2.521	0.012
Scored reaction	7	3	1.944	0.052	10	0	2.803	0.005
First vs Second playback	*N*	*T*	*Z*	*P*	*N*	*T*	*Z*	*P*
First response	9	9	1.599	0.110	11	29	0.356	0.722
First step towards	5	3	1.214	0.225	7	14	0.000	1.000
Response duration	8	15	0.420	0.674	11	28	0.445	0.657
Closest distance	4	5	0.000	1.000	8	11.5	0.910	0.363
Scored reaction	7	7	1.183	0.237	10	27	0.051	0.959

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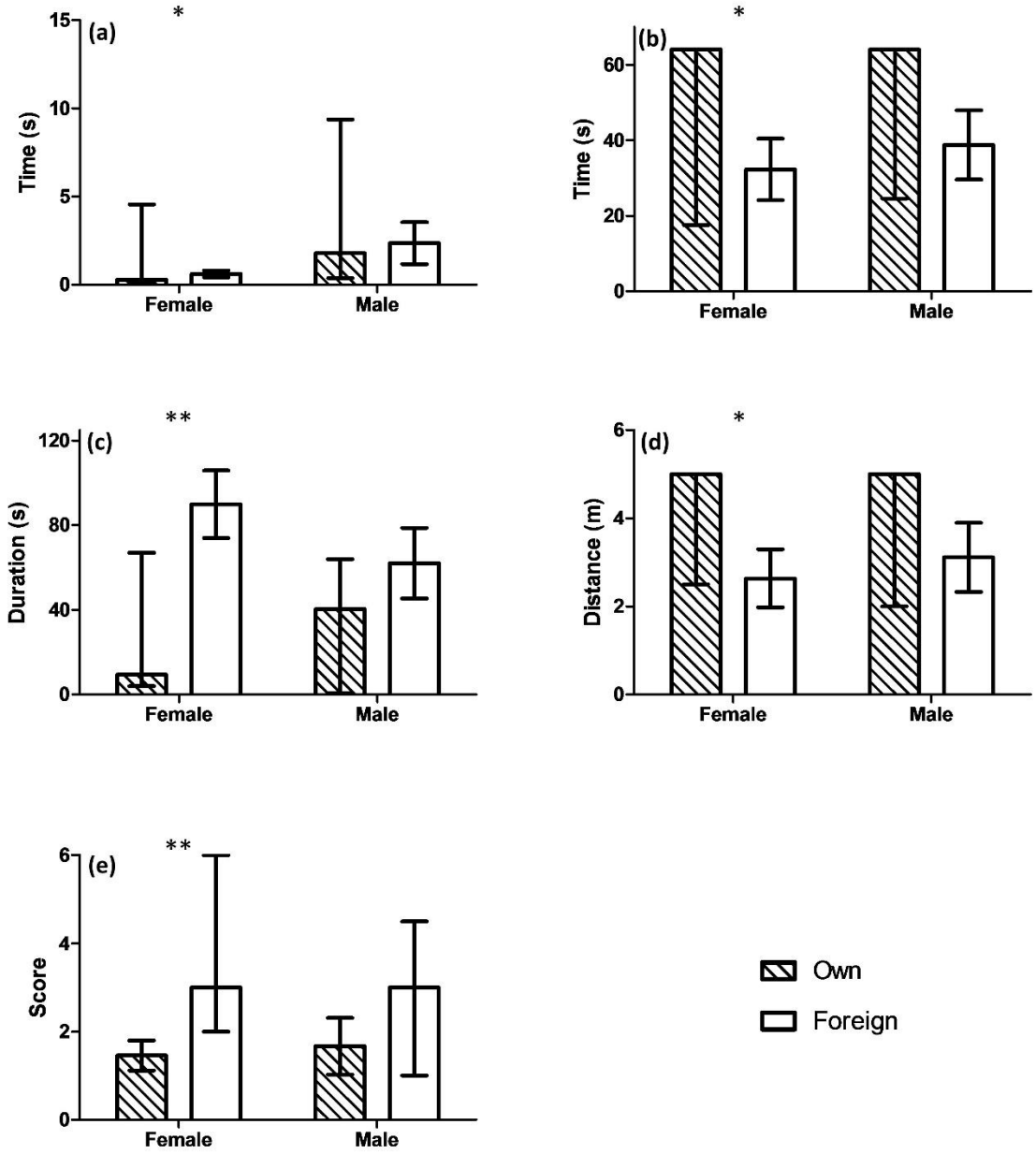

Figure 3.5: The target's median response to familiar callers (hatched bars) versus foreign callers (white bars) for female and male callers. Response variables were: a) time until first response, b) time until first step, c) response duration, d) closest distance to speaker and e) scored reaction (see Methods). Columns and error bars denote median and interquartile range. Stars indicate significance for Wilcoxon matched-pairs tests with *P<0.05 and **P<0.01.

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3.5 Discussion

Dwarf mongoose isolation vocalisations contain information about the caller's identity, sex and group within their acoustic structure and receivers are capable of discerning and using this information to tailor their responses. The difference we observed in the mongooses' response to own- versus extra-group individuals' isolation calls could be a consequence of the mongooses utilising either the group-specific or individually-specific characteristics of the call.

Individual distinctiveness within the structure of isolation vocalisations has been found in a number of species including Amazonian manatees (Sousa-Lima et al., 2002), domestic kittens, *Felis silvestris catus* (Scheumann et al., 2012), white-faced capuchins (Digweed et al., 2007), chacma baboons (Fischer et al., 2001, 2002) and several bat species including Mexican free-tailed bat pups, *Tadarida brasiliensis mexicana* (Gelfand & McCracken, 1986), spear-nosed bat pups, *Phyllostomus hastatus* (Bohn et al., 2007), and noctule bat pups, *Nyctalus noctula* (Knörnschild et al., 2007). Of these, only Mexican free-tailed bats, spear-nosed bats, Amazonian manatees and white-faced capuchins have been tested for and displayed discrimination based on these cues. Dwarf mongooses are known to be able to recognise individual group members from their contact (close) calls (Sharpe et al., 2013) and distinguish between group members based on their mobbing calls (Kern & Radford, 2016), so it is feasible that they were utilising individually-specific cues in isolation calls for recognition.

It seems unlikely that the mongooses were employing group-specific cues to distinguish between the calls of own- and extra-group conspecifics because not all groups exhibited a distinctive group signature. Consistent with this, there is no evidence that Herpestids employ group-specific acoustic signals. The recruitment calls of banded mongooses (*Mungos mungo*) show no discernible group-specificity (Furrer & Manser, 2009a) and meerkats (*Suricata suricatta*), which have a very similar social system to dwarf mongooses (Sharpe, Rubow & Cherry, 2016), do not respond to group differences in their close calls (Townsend, Hollén &

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Manser, 2010). Although group-specific signals are not uncommon in the long-distance calls of social mammals, especially those that live in an environment where acoustic signalling is the most efficient mode of communication (Townsend et al., 2010), they have been detected in only two studies of isolation vocalisations thus far: greater sac-winged bat pups, *Saccopteryx bilineata* (Knörnschild et al., 2012) and evening bat pups, *Nycticeius humeralis* (Scherrer & Wilkinson, 1993) exhibit family group signals. Gillam & Chaverri (2012) who studied inquiry and response calls of the Spix's disc-winged bat, *Thyroptera tricolor*, suggest that the high stability within bat social groups and territories may be why the species' contact calls show stronger individuality and weaker group-specificity. They argue that individuals need learn only the calls within their own group and respond to the familiarity of callers. This may also explain the acoustic findings for dwarf mongoose isolation calls.

Differences and similarities that we found in group acoustics could be due to vocal learning, morphology or genetic relatedness between individuals (Boughman & Wilkinson, 1998; Townsend et al., 2010). Townsend et al. (2010), suggest genetic similarity is responsible for the meerkat's group-distinctive contact calls having no apparent utility. Groups that are widely separated geographically may also be widely separated genetically and acoustically. In this study, the two mongoose groups which differed acoustically (Bugbears and Halcyon) were also those situated furthest from one another geographically (Fig. 3.3). Since females generally remain within their natal groups, any kin-related group signatures should become apparent when testing is limited to these individuals, but we still found no distinction between groups.

The finding that calls have sex-specific acoustic characteristics was unexpected for two reasons. Firstly, the social Herpestids do not display sexual dimorphism (Clutton-Brock et al., 2002; Sharpe, Jooste & Cherry, 2012), so one would expect no difference in the acoustics of male and female calls on morphological grounds. In addition, all previous studies on Herpestid acoustics that performed analysis for sex-related differences found no distinction between the calls of males and females (White, 2001; Furrer & Manser, 2009a; Jansen, Cant & Manser,

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2012). To our knowledge, this is therefore the first example in Herpestids where a vocalisation is specific to sex and audience members bias their response based on this information. Secondly, there is no clear reason why the mongooses would need to know the sex of a group member that has become separated. All group members, regardless of sex, contribute to all the group's cooperative activities and are, presumably, equally valuable (Rood, 1986). Similarly, there is a very strong likelihood that individuals are recognisable to their own group members via the individuality of their isolation calls, so a cue for sex would be redundant.

The sex-biased results of the playback experiments make it clear that the mongooses are using the sex-related cues in isolation calls (for unfamiliar conspecifics), and also give an indication of how these unexpected cues evolved. Mongooses are not only using isolation calls to reunite with their own group members but are also paying attention to the sex-specificity in the calls of foreigners. They are therefore eavesdropping on the vocalisations of neighbouring individuals that have become separated from their groups in order to exploit this information for their own purposes. Acoustic distinction between sexes would evolve if isolated individuals gain benefits (or avoid costs) as a result of neighbours being able to determine their sex from a distance. For example, as it appears from our results that males are of less interest to other groups than are females, it may benefit isolated males to advertise their sex to avoid any unnecessary and potentially dangerous encounters while alone. Furthermore, once sex-specific acoustic differences have evolved, the isolation call can be exploited by either sex to advertise for mates. This would explain why females have been observed to use the isolation vocalisation to call to transient males that approach their group, and dominant males use it to call their mates during mate-guarding (L. L. Sharpe, personal communication, 10 May 2015). Similarly, dwarf mongooses, who give isolation calls during intergroup encounters, may be doing so not only to reunite group members and coordinate group movement, but also to advertise their sex. This would reduce an individual's chance of suffering an attack because only individuals of the same sex engage in fights during intergroup encounters (Rood, 1986; Sharpe et al., 2012).

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These results are in accordance with the findings of the only other study of isolation calls in a cooperative species. Cottontop tamarin isolation calls (combination long calls) also contain sex specific cues and are used to attract both group-members and potential mates alike (Miller et al., 2004). It is noteworthy that isolation calls (which are normally used only in a very specific context) have been co-opted for mate-attraction in both of these distantly related species.

The finding that group members of both sex responded more strongly to the calls of female foreigners than those of male foreigners is presumably attributable to the social structure of dwarf mongoose groups. This species is highly territorial and during border disputes group members chase and aggressively expel same-sex intruders only (Rood, 1986). Female dwarf mongooses have far more to gain from preventing territorial incursions than males because, as the philopatric sex, they generally remain in their natal territory for life (Rood, 1990). Additionally, dispersing/transient females (being unable to join established groups; Rood, 1986) must annex a territory of their own so they directly threaten the group's territorial integrity. This would explain the strong response shown by female targets to an apparent female intruder. In contrast, male group members have less to gain from preventing territorial incursions because they normally emigrate at 2-3 years of age to join neighbouring groups (Rood, 1990). However, male targets responded strongly to the calls of a foreign female presumably because they perceived it as an extra-group mating opportunity.

Given the important role that isolation vocalisations play in maintaining group cohesion, it may appear incongruous that the dwarf mongooses varied greatly in their responsiveness to the isolation calls of their own group members, and only one-third of target mongooses actively sought out the caller. However, under natural conditions, it is normal for one or two group members only to respond to a lost individual, and this is all that is required for the isolated animal to relocate the group (Sharpe, personal observation). During the playback experiments, non-target group members also heard - and often responded to - the isolation call playbacks, potentially making a response by the target unnecessary. The decision to seek

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out missing group members and actively respond to their isolation calls appears to be related the degree of affiliation that group members share. A recent study of dwarf mongoose snake-mobbing recruitment calls found that individuals were more likely to respond to the mobbing calls of individuals with whom they spent more time grooming and foraging (Kern & Radford, 2016).

Aspects of the experimental design may also have contributed to the target mongooses' relatively weak response to its own group member's calls. For example, the 'own-group' playback could have generated a 'violation of expectations' (Townsend, Allen & Manser, 2011), if the target mongoose recognised the caller and realised that it was not in fact isolated but present within the group. No such violation would occur during the playback of foreign calls. Townsend et al. (2011) demonstrated that meerkats recognise, and respond to, such incongruities during the playback of contact (close) calls, but Jansen, Cant and Manser (2013) found that banded mongooses do not. Although we only played isolation calls when the donor of the call was not within sight of the target, it is possible that the two animals were within auditory range and that the target recognised the incongruity and modified its response. However, such violations of expectations cannot account for the large difference in response between own group and foreign calls, or we would have observed this difference for both male and female callers, not just females.

Another factor that may have affected the relative strength of response was the proximity of the speaker to the target. The chosen distance (5 m), while close, was within the natural range for these calls. Nevertheless, target mongooses may have responded less strongly to group members' isolation calls because the 'lost' caller was not far off and could therefore find its way back to the group unaided. Conversely, foreigners calling at such a distance, may have been perceived by the target as threateningly close to the group and thus worthy of a strong response. Although speaker proximity may have accentuated differences in the targets' responses, it remains clear that the dwarf mongooses could differentiate between own and foreign callers – the purpose of the experiment.

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In retrospect, our study was constrained by the limited number of habituated groups. There are a few remaining uncertainties which could be resolved by analysing calls from a larger sample of groups in a larger area. For example, the level of intensity in the response of target mongooses varied greatly and this may have had multiple causes including group size, individual motivation or season. Members from smaller groups may be more vulnerable when losing group members or encountering foreigners, whereas larger groups may be more confident in responding to opposing groups. Season may play a role as mongooses may be more eager to encounter potential mates during oestrus or more defensive when the group has pups. For this reason no playbacks were conducted while the dominant female was in oestrus or during the first three weeks after a litter was born.

In conclusion, this study not only provides the first investigation into isolation calls in a cooperatively breeding carnivore, but also provides the first evidence of an Herpestid exhibiting and utilising sex-specificity in a vocalisation. In addition to sex-specific cues, dwarf mongoose isolation calls also provide cues that allow the audience to distinguish group members from other conspecifics.

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Chapter 4:

A comparison of individual distinctiveness in three vocalisations of the dwarf mongoose (*Helogale parvula*)

(Submitted to *Ethology* for publication)

4.1 Abstract

Individual-specificity can be found in the vocalisations of many avian and mammalian species. However, it is often difficult to determine whether these vocal cues to identity rise from 'unselected' individual differences in vocal morphology or whether they have been accentuated by selection for the purposes of advertising caller identity. By comparing the level of acoustic individuality of different vocalisations within the repertoire of a single species, it is possible to ascertain whether selection for individual recognition has modified the vocal cues to identity in particular contexts. We used discriminant function analyses to determine the level of accuracy with which calls could be classified to the correct individual caller, for three dwarf mongoose (*Helogale parvula*) vocalisations: snake, isolation and contact calls. These calls were similar in acoustic structure but divergent in context and function. We found that all three call types showed individual-specificity but levels varied with call type (increasing from snake to contact to isolation call). The individual distinctiveness of each call type appeared to be directly related to the degree of benefit that signallers were likely to accrue from advertising their identity within that call-context. We conclude that dwarf mongoose signallers have undergone selection to facilitate vocal individual recognition, particularly in relation to the species' isolation call.

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4.2 Introduction

Individually distinctive vocalisations are widespread in terrestrial vertebrates, primarily because of individual variation in vocal tract morphology (Scherrer & Wilkinson, 1993; Taylor & Reby, 2010; Gillam & Chaverri, 2012). Researchers have demonstrated that myriad bird and mammal species exploit identity cues and are able to distinguish between conspecifics based solely on their vocalisations (Tibbetts & Dale, 2007). The evolution of vocal individual recognition (or at least the recognition of classes of individual, such as group member, kin or neighbour) occurs as a result of selection operating on the receiver or the signaller, or both. If receivers derive a benefit from distinguishing between individual callers (on the basis of sex, rank or group membership, for example), selection is likely to favour an enhancement in the receivers' ability to perceive, learn and recognise the vocal traits that characterise that class of individual. For example, cottontop tamarins (*Saguinus oedipus*), which emit 'complex long calls' when seeking potential mates, show a sensory bias for the vocal traits present in the long calls of opposite-sexed conspecifics (Miller, Scarl & Hauser, 2004).

Selection will also operate on the signaller whenever it is costly for a caller to be confused with other conspecifics (Dale, Lank & Reeve, 2001). Under such circumstances, selection will favour the strengthening of the signaller's individual vocal distinctiveness (Beecher, 1982). In colonial-nesting cliff swallows (*Hirundo pyrrhonota*), for example, the individual distinctiveness of the chicks' calls is 20 times greater than that found in the calls of barn swallow (*H. rustica*) chicks. Barn swallows nest solitarily and so – unlike cliff swallows – there is no risk that a chick's parents will fail to recognise it in the crowd (Loesche, Stoddard, Higgins & Beecher, 1991).

Much of the extensive research on vocal recognition has focussed primarily on receivers, presumably because it is relatively straightforward to test their perceptual abilities and discriminatory behaviour using playback experiments (Tibbetts & Dale, 2007). Far fewer studies have examined vocal recognition from the perspective of the signaller. One probable

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reason for this is the difficulty of differentiating between simple vocal cues of identity (which arise from 'unselected' individual differences in vocal morphology) and genuine *signals* of identity (i.e. individual vocal traits that have been accentuated by selection for the purposes of advertising identity; Bergman & Sheenan, 2013).

One way to ascertain whether selection for individual recognition has enhanced a signallers' vocal distinctiveness is by comparing different call types within a single species. The benefit that a signaller derives from advertising its identity will vary with context: an individual calling its alliance partner for assistance during a fight will benefit only if its vocal identity is unmistakable, yet the same individual gains little from proclaiming its identity in a predator warning and may suffer a cost if its food-associated call is identity-specific and dominant individuals exploit this to commandeer its meal. These context-related differences in the benefit that signallers derive from revealing their identity should be reflected in the degree to which different calls (from diverse contexts) exhibit individual distinctiveness. For example, in banded mongooses (*Mungos mungo*) - a species in which individual pups are often cared for by a single adult 'escort' – both the pup and escort maintain their association and can recognise one another's contact and distress calls, respectively. However, pups (who gain considerable benefit from being escorted) show twice the degree of individual distinctiveness in their calls than do escorts, who suffer an energetic cost from escorting a youngster (Müller & Manser, 2008).

A number of other studies have found that the individual-specificity of a species' vocalisations varies with call type or call context (Mitani, Gros-Louis & Macedonia, 1996; Rendall, Owren & Rodman, 1998; Charrier, Jouventin, Mathevon & Aubin, 2001; Yin & McCowan, 2004; Bastian & Schmidt, 2008; Rendall, Notman & Owren, 2009; Leliveld, Scheumann & Zimmermann, 2011; Lemasson & Hausberger, 2011; Bouchet, Blois-Heulin, Pellier, Zuberbühler & Lemasson, 2012; Gillam & Chaverri, 2012; Warrington, McDonald, Rollins & Griffith, 2014; Humphries, Finch, Bell & Ridley, 2016). However, few of these studies have examined how these differences relate to signaller benefits, either because good information about call

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function/context is lacking or the study focusses on other research questions. Nevertheless, several studies have examined whether their findings support the two hypotheses (mutually non-exclusive) that have been advanced to explain the evolution of individually recognisable calls. The first is the 'visual contact' hypothesis, which posits that calls associated with long-distance communication will be more individually distinctive than short-range calls, because separated individuals do not have access to additional (visual or olfactory) cues to caller identity (Insley, 1992; Mitani et al., 1996). Supporting this hypothesis, the long-distance pant-hoots of chimpanzees (*Pan troglodytes*) are more individually distinctive than their short-range pant-grunts (Mitani et al., 1996). Similarly, the contact coos used by separated rhesus macaques (*Macaca mulatta*) have greater individual-specificity than their 'face-to-face' grunts (Rendall et al., 1998). However, the long-distance calls of gray mouse lemurs (*Microcebus murinus*) and red-capped mangabeys (*Cercocebus torquatus*) are no more individually distinctive than their short-range calls (Leliveld et al., 2011; Bouchet et al., 2012). Similarly, the isolation barks of domestic dogs (*Canis familiaris*) do not differ in individual distinctiveness from barks given during play (Yin & McCowan, 2004).

The second hypothesis – the 'social function' hypothesis - posits that individual distinctiveness will be greater in vocalisations used to mediate social interactions (contact calls, agonistic calls) than vocalisations used in other contexts (alarm calls, group-advertisement calls) (Charrier et al., 2001) because the development and maintenance of complex social relationships is greatly facilitated by individual recognition (Shapiro, 2010). In support of this hypothesis, the contact calls of south polar skuas (*Catharacta maccormicki*) and Campbell's monkeys (*Cercopithecus campbelli*) are more individually distinctive than are their alarm calls (Charrier et al., 2001; Lemasson & Hausberger, 2011). Similarly, in a study of red-capped mangabeys, the highest levels of individual specificity were found in calls that mediate intragroup social interactions (Bouchet et al., 2012). However, this was not the case in gray mouse lemurs (Leliveld et al., 2011).

The apparently contradictory findings of these studies (most of which compare vocalisations that differ widely in acoustic characteristics) may be a consequence of the confounding effect

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of call structure. There is growing evidence that harmonic calls (those with narrow frequency bands) are better able to convey individual indistinctiveness than noisy calls (those with a broad frequency band) because they can transmit additional information via frequency modulations, rather than just via amplitude modulations (Wiley & Richards, 1978). Several studies have found that individual distinctiveness decreases with an increase in the noisiness of the tested call type (Rendall et al., 1998, 2009; Bastian & Schmidt, 2008; Leliveld et al., 2011).

In this study we compare levels of individual distinctiveness within three dwarf mongoose (*Helogale parvula*) vocalisations that are very similar in acoustic structure but differ considerably in context, function and receiver response. All three calls consist of a single element that is relatively short in duration and pure in tone, with little to no modulation in pitch. Therefore we avoid any confounding impact of diverse call structures. We assess one short-range, intragroup social call (the 'contact call'), one predator warning call (the 'snake call', which also has a recruitment function) and one long-distance call used when a mongoose becomes separated from its group (the 'isolation call'). Previous experimental work has demonstrated that dwarf mongooses discern and differentiate between individual callers for all three vocalisations (Sharpe, Hill & Cherry, 2013; Kern & Radford, 2016; Chapter 3).

Firstly, we examine whether there is evidence that selection has favoured the enhancement of individual distinctiveness in these dwarf mongoose vocalisations. If the individual variation found in these calls is simply a product of 'unselected' morphological variation (i.e. simple vocal cues; Bergman & Sheenan, 2013), we would expect the degree with which calls can be correctly classified to individual caller will not differ with call type. Additionally, the most important acoustic cue to individuality (e.g. call pitch) should be very closely correlated across all three call types for individuals. If the level of individual distinctiveness differs between call types (suggesting that selection for identity signalling has occurred), we will examine whether these differences reflect the likely benefits (or costs) that signallers obtain from advertising their identity within the different call contexts. We will also assess whether the differences in

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individual distinctiveness between call types are supportive of the 'visual contact' hypothesis and the 'social function' hypothesis.

4.3 Methods

4.3.1 Study species:

Dwarf mongooses are small (<300g) cooperative breeders in the Herpestid family. They live in close-knit social groups (<30 individuals) in the savannah-woodlands of southern Africa (Caro & Stoner, 2003; Sharpe, Joustra & Cherry, 2010). Each group defends a territory of about 40 ha, in which they forage by day, as a loosely dispersed group (Rood, 1986; Sharpe, Jooste & Cherry, 2012). Dwarf mongooses feed primarily on arthropods, though they also eat small birds, reptiles and rodents when given the chance (Rasa, 1983; Rood, 1990). Due to their small size, foraging mongooses are often obscured from one another by dense vegetation. Like other mongoose species, they are vulnerable to predation by small to medium-sized mammals, snakes and raptors (Manser et al., 2014).

4.3.2 Study vocalisations:

As dwarf mongooses are highly social and must maintain contact with one another in dense vegetation, they have developed a sophisticated system of vocal signalling consisting of at least 25 different call types (Manser et al., 2014). These include more than 14 predator alarm calls that are functionally referential and convey information about both predator type and degree of threat (Beynon & Rasa, 1989; Manser et al., 2014). In this study we focus on three specific calls: the contact call, the snake call and the isolation call (Fig. 4.1).

The contact call (Fig. 4.1a) is a close range call used to maintain contact between group members while they are foraging or moving (Sharpe et al., 2013). It consists of a single, low peep (730.4-1714.4 Hz) of short duration. Experiments have revealed that group members exhibit 'true' individual recognition using contact calls (Sharpe et al., 2013).

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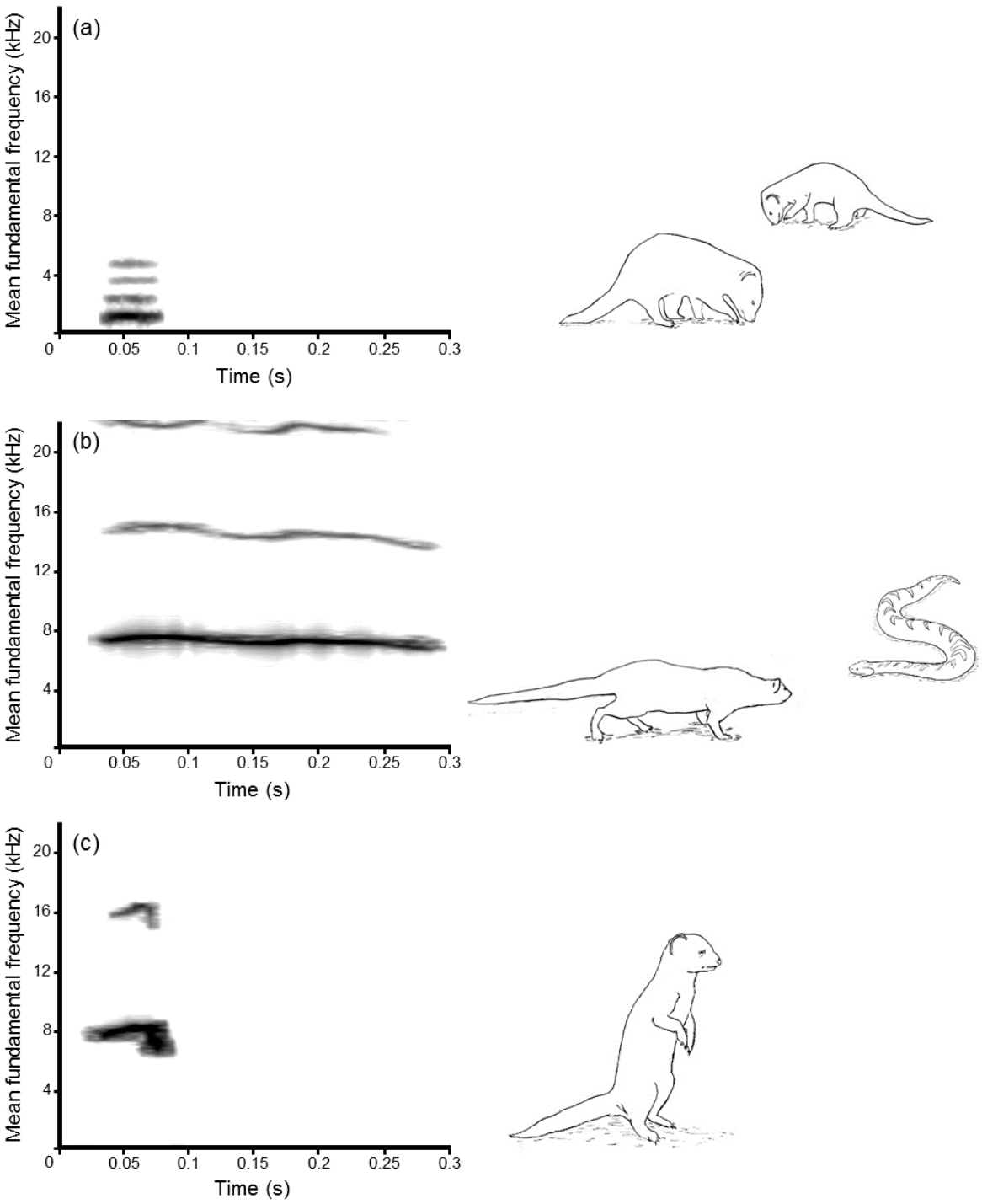

Figure 4.1: Spectrographs and diagrams of behaviour typically associated with the (a) contact call, (b) snake call and (c) isolation call of an adult male dwarf mongoose (ID code: EM063). Spectrographs were prepared in Raven Lite 1.0 at 50% brightness, 60% contrast and spectrogram sharpness 512 pts. (Diagrams by Kyle Kulenkampff.)

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The snake call (Fig. 4.1b) is a warning call emitted by a group member when it encounters a snake. This vocalisation consists of a single, high-pitched squeak (6153.0-8369.0 Hz). Group members respond by cautiously investigating nearby vegetation and – once the snake is pinpointed - teaming up to mob the reptile (Chapter 2). Dwarf mongooses are able to differentiate between the snake calls of different group members, responding more strongly to callers with whom they share a strong social bond (Kern & Radford, 2016).

The isolation call (Fig. 4.1c) is a recruitment call emitted when a group member becomes separated from the group. It consists of a single, high-pitched squeak (5931.5-9000.2 Hz) which sounds indistinguishable from the snake call to the human ear, but which differs acoustically (Chapter 2). The isolation call serves to facilitate the lost individual's reunion with its group, and experiments have revealed that the mongooses discriminate between callers on the basis of sex and group membership (Chapter 3).

In this study we examined the contact, isolation and snake calls derived from each of 18 wild, adult (>12 months old) dwarf mongooses from 3 groups (5, 6 and 7 individuals respectively per group). These groups (mean group size: *N*=16) form part of a dwarf mongoose population that is habituated to observers on Phuza Moya Private Game Reserve in south eastern Limpopo, South Africa (24°16'10''S, 30°47'46''E; elevation 470 m).

4.3.3 Sound recording:

We recorded vocalisations between March of 2015 and 2016 by following foraging groups on foot (at a distance of 0.5 to 3 metres) in the morning and recording each call type opportunistically. When vocalisations were heard, the caller was approached and identified (all group members bore individually unique blonde hair-dye marks). Calls were recorded with Sennheiser directional microphones (model ME66/K6) and a Marantz PMD-670 solid state recorder or Roland R26 portable recorder. Sampling was done only on calm sunny days (wind speed <11 km/h) to maximise recording quality.

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Due to the rarity of natural snake encounters, we staged an artificial snake encounter at each group using an adult (>4 years old) male puff adder from the Kinyonga Reptile Centre in Hoedspruit. This was done under the supervision of a trained employee of the centre who was responsible for all handling and transport of the snake. The snake was contained in a mesh cage (55 x 75 x 46 cm) at all times to ensure its own safety and that of the mongooses and observers. We placed the cage within the trajectory of the foraging mongooses, in a shaded area where puff adders may naturally occur. This setup provided visual, olfactory and auditory cues to which the mongooses could respond. We began recording before the leading mongoose encountered the snake and terminated recording once all mongooses had moved past it. Each time a new caller discovered the snake and emitted recruitment calls, we noted the identity of the mongoose. The presentation procedure was approved by the ethics committee of Stellenbosch University (SU-ACUD16-00016) and had no lasting effects on the subjects.

We digitised all recordings at 16 bit, 48 kHz in .wav format for call extraction in Adobe Audition 2.0. We identified and extracted 304 snake calls (number per individual caller: 5 to 47), 513 isolation calls (5 to 92) and 191 contact calls (5 to 16) from the same 18 individuals. Only monosyllabic, high quality calls from individuals >6 months old were extracted for analysis. We considered calls to be of sufficient quality when they had a good signal to noise ratio with no obscuring background noise (such as other mongoose calls, bird calls, cicada chirps or wind) and at least two frequency bands were clearly visible. Using Luscinia bioacoustics software (RF Lachlan version 2.0) , we analysed calls by Fast Fourier Transformation with the following settings: 1024 points, Hamming Window, time step 0.36 ms, frame length 23.22 ms and overlap 98.45%. We analysed parameters that have been previously identified as important in determining individuality in the calls of dwarf mongooses (Chapter 3). For both the fundamental frequency and the first formant above it (Fig. 4.2), we measured the following parameters: overall peak, minimum and maximum frequency and the mean frequency at the mean, peak, maximum and minimum of the call. For the fundamental

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frequency alone, we additionally measured the duration, mean entropy and first and third quartiles of the power spectrum.

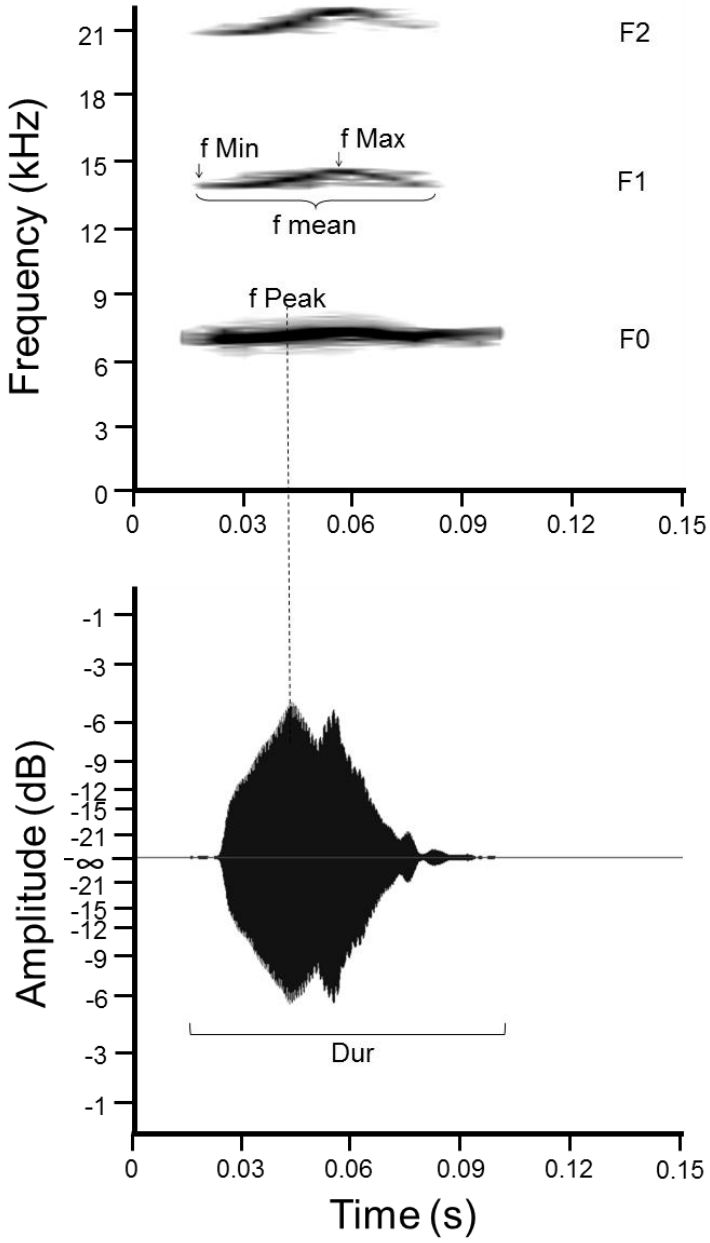

Figure 4.2: Spectrograph and waveform of a dwarf mongoose vocalisation depicting a few basic parameters measured on the fundamental frequency (F0) and first formant (F1). These are the duration (Dur); maximum (f Max), minimum (f Min) and mean (f mean) frequencies (shown on F1); and the peak frequency (f Peak) which is the frequency at the loudest amplitude of the call.

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Statistical analysis:

To identify whether snake, isolation and contact calls differ between individuals and the extent to which they can be classified correctly to the individual, we performed multivariate analyses of variance (MANOVA) in STATISTICA 64 v13; and stepwise discriminant function analyses with leave-one-out cross-validation (DFA) in IBM SPSS v23 respectively. Each DFA was analysed by adjusting the prior probabilities, accounting for varying number of calls per individual. As the data were not normally distributed and correlated, we first computed principal components for each call type and used those with Eigenvalues >1 in the subsequent analyses. For snake calls the first three principal components had sufficient eigenvalues and had a cumulative variance of 93.02%. Both isolation and contact calls had two principal components with cumulative variances of 89.54% and 84.64% respectively.

To identify whether the frequency of an individual's calls remained consistent across the three call types, we compared the mean peak fundamental frequency of the calls using Pearson's product-moment correlations (pairwise by call type). We chose this acoustic parameter because it is important for individual distinctiveness in all three call types.

4.4 Results

Individual dwarf mongooses differed significantly from one another with regards to their snake, isolation and contact calls (Table 4.1 MANOVA results), but the DFAs revealed that the accuracy with which calls can be classified to the individual was moderate and increased from snake (31.9%) to contact (41.4%) to isolation (51.3%) calls (Table 4.1 DFA results). Calls from all three types were classified to the individual with a higher accuracy than expected by chance (5.6%).

There is no clear trend with regards to misclassification of calls for any of the three call types. The most likely source of misclassifications would be within a sex in the same group or

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between individuals of similar age in different groups. This was however not the case for any of the three DFAs.

Table 4.1: The difference between individuals (MANOVA) and percentage of calls correctly classified to the individual (DFA) of the three dwarf mongoose call types

	MANOVA			DFA	
	F	*df*	*P*	Original	cross-validated
Snake calls	11.213	51, 846	<0.0001	34.50%	31.90%
Isolation calls	69.633	34, 988	<0.0001	52.40%	51.30%
Contact calls	23.601	34, 344	<0.0001	45.50%	41.40%

Two vocal parameters were consistently important in determining individuality in the first component of each vocalisation: the mean peak frequency of the fundamental and mean frequency of the first formant. In the second and third principal components, Wiener entropy and the overall minimum frequency of the fundamental played important roles. The most important factors for individuality were the F1 mean peak frequency, F1 mean frequency (measured at the mean) and the F0 mean peak frequency for snake, isolation and contact calls respectively. The loading for each factor (>0.5) can be seen in Table 4.2.

The mean peak fundamental frequency of an individual's calls was significantly correlated between each call type. Isolation calls were correlated to contact calls (Pearson's product-moment correlation: R=0.658, N=18, P=0.003) and snake calls (Pearson's product-moment correlation: R=0.579, N=18, P=0.012). The mean peak fundamental frequency of snake calls was more strongly correlated to that of contact calls (Pearson's product-moment correlation: R=0.812, N=18, P<0.0001).

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Table 4.2: Parameter loadings (<0.5) of the Principal Components Analyses for snake, isolation and contact calls. The highest two loadings in each component are highlighted in bold.

	Snake call			Isolation call		Contact call	
Parameter	PC 1	PC 2	PC 3	PC 1	PC 2	PC 1	PC 2
F0 Duration		**0.729**	**0.544**				0.617
F0 Peak f (overall)	0.954			0.964		-0.950	
F0 Min f (overall)	0.707	**-0.547**		0.671	**0.649**		**-0.808**
F0 Max f (overall)	0.867			0.921		-0.910	
F0 Peak f (mean)	0.986			**0.993**		-0.730	-0.503
F0 Mean f (mean)	0.983			0.992			**-0.805**
F0 Max f (mean)	0.945			0.973		-0.872	
F0 Min f (mean)	0.813			0.840		-0.790	
F0 PS Q1	0.967			0.970		-0.944	
F0 PS Q3	0.969			0.980		-0.935	
F0 Entropy (mean)			**0.947**		**0.881**	-0.937	
F1 Peak f (overall)	0.947			0.958		-0.949	
F1 Min f (overall)	0.885			0.829		-0.959	
F1 Max f (overall)	0.940			0.933		**-0.965**	
F1 Peak f (mean)	**0.991**			0.992		-0.957	
F1 Mean f (mean)	**0.991**			**0.993**		**-0.964**	
F1 Max f (mean)	0.956			0.973		-0.960	
F1 Min f (mean)	0.901			0.920		-0.867	

4.5 Discussion

All three types of dwarf mongoose vocalisation were distinctive between individuals, and single calls could be classified correctly to caller with moderate accuracy. However, the degree of individual distinctiveness differed between call types - increasing from snake to contact to isolation calls - suggesting that selection pressure has enhanced (or suppressed) individual distinctiveness within specific contexts.

Vocal cues to identity are primarily a consequence of individual variation in the morphology of an animal's vocal folds and supra-laryngeal vocal tract (Rendall et al., 1998). Therefore, it

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is not surprising that the pitch of calls emitted by an individual mongoose (measured as the mean peak frequency of the fundamental frequency band) was significantly correlated across all call types. However, the strength of this correlation varied. The pitch of an individual's snake and contact calls were very closely related (r = 0.81) despite differences in call structure (Fig.4.1a & b), suggesting that the identity cues within these call types were probably a simple consequence of vocal morphology. However, the correlation was weaker for isolation calls, particularly between isolation and snake calls (r = 0.58). Given the structural similarity of these call types (Fig 4.1b & c), it would appear that signallers were modifying the 'baseline' vocal identity cues within their isolation calls, possibly to enhance the individual specificity of their signals. This would explain the relatively high level of individual distinctiveness observed within isolation calls.

The degree of individual distinctiveness found within each call type appeared to reflect the benefits that signallers may gain from proclaiming their identity. Snake calls – used to warn other group members when a snake is detected - offered signallers little incentive to advertise identity and showed the lowest level of individual distinctiveness. This call also serves a recruitment function, with receivers initially searching for the snake and then banding together to mob the reptile (Chapter 2). Individuals are known to respond more strongly to the snake calls of companions (those with whom they most often allo-groom and forage; Kern & Radford 2016), but a signaller is unlikely to benefit directly from receiver response (regardless of its strength) because it is not at risk (i.e. it knows the snake's location, and snakes only catch mongooses if they can take them unawares; Sharpe, pers. comm.).

It has been proposed that, in situations where call context is of greater importance than caller identity (e.g. predator warning calls, such as the snake call), selection will act to suppress individual vocal distinctiveness so as to reduce signal ambiguity and facilitate a rapid response by receivers (Shapiro, 2010). Such selection pressure can only influence a signaller's calls indirectly, through kin selection (Hamilton, 1964), or via the benefits derived from group augmentation (Kokko, Johnstone & Clutton-Brock, 2001). However, because most members

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of dwarf mongoose groups are close relatives (Keane, Creel & Waser, 1996), this selection pressure may have contributed to the lower levels of individual distinctiveness observed in snake calls.

Of the three call types evaluated in this study, contact calls exhibited an intermediate level of individual distinctiveness, although this level is sufficient to allow 'true' individual recognition (Sharpe et al., 2013). Contact (close) calls are emitted by all individuals when the group is foraging or travelling, and the call is used to maintain contact, negotiate spacing and avoid aggressive confrontations between group members (Sharpe et al., 2013), particularly when visibility is poor due to dense vegetation. Advertising identity within contact calls appears to provide signallers with both costs and benefits. Dwarf mongooses prefer to forage in the company of individuals with whom they share strong social ties (Sibun, 2014). Because these 'bonded' individuals are more likely to come to one another's aid (Kern & Radford, 2016) and dwarf mongooses often intervene when a group member is captured by a predator (successfully rescuing one-third of all raptor-victims; Rasa, 1987), signallers will derive a very appreciable benefit from producing identifiable contact calls that allow 'bonded' group-mates to pinpoint their location and remain close by. Conversely, providing clear identity cues is likely to carry a significant cost in the winter dry season. During this period of prey scarcity, dwarf mongooses frequently indulge in kleptoparasitism, stealing prey from group members of lower rank than themselves (Sharpe, Rubow & Cherry, 2016). A signaller that provides individually-distinctive contact calls will therefore be advertising its location (and vulnerability) to all potential thieves (i.e. higher-ranking group members). Under these circumstances, we would expect the individual distinctiveness of contact calls to be positively correlated with social rank, and qualitative observations confirm that the contact calls of alpha mongooses are far more distinctive than those of lower ranking group members.

Unlike the other call types examined in this study, the isolation call – which showed the highest level of individual distinctiveness - appears to provide signallers with unequivocal incentive to advertise identity. Emitted by individuals that have become inadvertently separated from their group, this long-distance call is used to notify the group and facilitate a

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reunion (Chapter 3). As in all the obligate, social Herpestids, lone individuals outside their group are very vulnerable to predation and suffer high levels of stress (e.g. Young et al., 2006; Young & Montfort, 2009). To maximise the speed with which a reunion can be effected, lost individuals need to produce isolation calls that are immediately recognisable by group members. Providing unmistakeable vocal cues to identity will ensure a prompt response from 'bonded' group members, who will then seek out the lost caller. Highly-valued group members, such as the group's alpha pair, would particularly benefit from providing individually distinctive isolation calls. In white-faced capuchins (*Cebus capucinus*), for example, group members respond to the lost calls of dominants more often than to the calls of subordinate individuals (Digweed, Fedigan & Rendall, 2007). Dwarf mongooses are likely to show a similar bias toward dominant individuals because they do so in other contexts (Sharpe et al., 2013; Kern, Sumner & Radford, 2016).

The relatively high level of individual distinctiveness apparent in dwarf mongoose isolation calls is supportive of the 'visual contact' hypothesis (Mitani et al., 1996) which asserts that long-distance calls need to be more individually distinctive than short-range calls because receivers do not have access to alternative cues to caller identity. However, the mongooses' snake calls were also used to alert dispersed group members (foraging well beyond the visual and olfactory range of the caller), yet these warning calls were less individually distinctive than the mongooses' short-range contact calls. Our findings also do not support the 'social function' hypothesis (i.e. individual distinctiveness will be greatest in calls used to mediate intragroup social interactions), because the mongoose's contact calls were less individually-specific than their isolation calls.

We conclude that dwarf mongooses have undergone selection to enhance the individual distinctiveness of their vocalisations, and that this is particularly pronounced in the case of the species' isolation call. It appears that the degree to which vocal individuality is augmented directly reflects the degree of benefit that signallers derive from revealing their identity vocally within different call contexts.

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Chapter 5:

Conclusion

Many animal signals convey information beyond their primary purpose. This extends to Herpestid vocalisations (see Manser et al., 2014 for review of papers on mongoose vocalisation). Of the three most commonly studied herpestids, there is a surprising lack of information on the vocalisations of dwarf mongooses, even though this species has at least 30 discrete vocalisations (Manser et al., 2014), is highly social and lives in a densely vegetated environment (Rasa, 1987) where vocal signals are critical. This made them an ideal species in which to study the information conveyed by vocalisations and how it effects conspecifics. Based on the literature, long-distance vocalisations are expected to contain information to aid receivers in making more rapid and appropriate decisions (Gersick, Cheney, Schneider, Seyfarth & Holekamp, 2015). The long-range recruitment vocalisations of dwarf mongooses were therefore the perfect place to begin examining acoustic information in this species.

This study investigated the information conveyed by dwarf mongoose recruitment calls and the behavioural responses they elicit. It was predicted that the context that prompted a recruitment call would influence the acoustic structure and, in turn, the response of receivers. Furthermore, it was predicted that a specific recruitment call type, the isolation call, would additionally provide receivers with cues about the identity of the caller.

Because both the acoustic structure and response to informative cues are important (Townsend, Hollén and Manser, 2010), acoustic analyses were performed in conjunction with playback analyses.

The overall finding was that dwarf mongoose recruitment calls convey information, not only about the context in which the call was produced (chapter 2), but also about the identity of caller (chapter 3). The level to which identity is expressed is dependent on the context (chapter 4).

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In chapter 2 the most common recruitment vocalisations, isolation and snake calls, were compared. In contrast to banded mongoose recruitment calls which are graded according to urgency and are harsh and low in tone (Furrer & Manser, 2009a), dwarf mongoose recruitment calls are context specific (refer to caller or situation) and have a purer (smaller bandwidth) tone. Individuals responded faster and more strongly to snake than isolation calls, approaching closer to the speaker when snake calls were heard. Snake calls also elicited specific responses, head-bobbing and creeping, which isolation calls did not. These calls are therefore functionally referential as they not only refer to context but also incite differing responses, as is the criteria explained by Macedonia and Evans (1993). The differing recruitment system (referential versus urgency-based) in dwarf mongooses versus other Herpestids has implications on the evolution and development of recruitment calls within a family of species.

Chapter 3 examined isolation recruitment calls specifically. It is the first investigation of such calls in the family *Herpestidae*. Isolation calls inform the receiver about the caller's identity, sex and potentially also group-membership. This corresponds with dwarf mongoose contact calls, from which receivers are able to identify and bias their response to specific individuals (Sharpe, Hill & Cherry, 2013). The results of this chapter are also supported by acoustic findings in meerkat and banded mongoose contact calls, which are individually distinct (Townsend, Allen & Manser, 2011; Fitch, 2012). However, banded mongooses do not use these acoustic cues to discriminate between individuals. Though meerkat contact calls also contain group-specific information, group members do not respond differently to different group-signatures (Townsend et al., 2010). As dwarf mongooses responded more strongly to foreign females, this is the first evidence of sex-bias in response to vocalisations in an Herpestid.

In chapter 4 the level of individual-specificity in dwarf mongoose vocalisations was examined. Playback presentations have shown that both isolation calls (chapter 3) and snake calls (Kern & Radford, 2016) are used to distinguish between individuals. It was however unclear whether

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these calls convey individuality to the same extent. It was also unknown whether individuality in dwarf mongoose vocalisations was merely a function of variation in vocal tract morphology or due to the function of each call type. The level of individual-specificity in snake and isolation calls was therefore compared to that in contact calls – the only other vocalisation in which individual recognition has been proven. Individual-specificity increased from snake to contact to isolation calls. Selection for individuality in dwarf mongoose calls is therefore a function of call context and the benefit of successfully conveying caller identity, over and above individual variation in morphology.

This study examined only two of the contexts in which recruitment calls are produced and can therefore not make conclusions about all contexts or all dwarf mongoose vocalisations. This was mainly due to the rarity of recruitment calls in general. The infrequency of recruitment calling events also limited the sample of vocalisations that could be recorded. Finally, the study was limited by the number of groups in which sampling took place. More groups would allow for a more comprehensive examination of group and distance-related differences between callers. However, the time constraints imposed by an MSc study, the set number of long-term habituated groups (four) and the small number of researchers at the site (two) made a larger sample of calls difficult to obtain and a larger sample of groups difficult to maintain.

It is the nature of research to generate more questions than have been answered. It may be worth undertaking a longer term study with a larger study population to obtain an even better understanding of dwarf mongoose recruitment calls. Suggested areas for further examination include: a) differences in acoustics and response to recruitment calls under more contexts; b) responses of dwarf mongooses to different species of snakes – including predatory and/or edible species; c) differences in isolation call cues between geographically separate versus adjacent groups and populations; and d) comparison of identity cues in the acoustics of a greater representation of the dwarf mongoose vocal repertoire..

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The findings of this study highlight the need to examine closely vocalisations that appear superficially similar to ascertain their purpose. It confirms the necessity to perform both acoustic analysis and playback-response analysis to identify not only whether informative cues exist, but also whether their presence is significant and meaningful to conspecifics. Furthermore, this study has added significantly to the knowledge available not only on Herpestid acoustics but dwarf mongoose vocalisations specifically.

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